

AN ABSTRACT OF THE THESIS OF

Roy E. Beaty for the degree of Master of Science in Fisheries Science presented on February 18, 1992. Title: Changes in Size and Age at Maturity of Columbia River Upriver Bright Fall Chinook Salmon (*Oncorhynchus tshawytscha*): Implications for Stock Fitness, Commercial Value, and Management

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The average size and age of chinook salmon (*Oncorhynchus tshawytscha*) caught in commercial fisheries along the Pacific Coast of North America have decreased substantially in this century. These declines might be caused in part by changes in size and age at maturity within the stocks contributing to those fisheries. Upriver Brights (Brights), a stock of fall chinook salmon in the Columbia River, are one of those stocks. The purposes of this study were to (1) determine if average size and age at maturity of Brights have declined, (2) gain a better understanding of the factors that may contribute to such declines, and (3) describe potential consequences of these changes.

Data from in-river fisheries suggest that the average weight of mature Brights returning to the Columbia River has decreased approximately 2.7 kg since the 1910s, an average rate of about 0.1 lb·yr⁻¹ (45 g·yr⁻¹). Most of the potential biases in these data tend to make this estimate conservative. Insufficient data were available to describe changes in average age at maturity.

There are many potential causes for the decline in average size of mature Brights, including factors that affect very early life stages. Other researchers have determined that size at maturity appears to be highly influenced by inheritance, gender, and growth rate. I describe how maternal size can influence -- through time of spawning, choice of spawning site, and egg size -- the viability of the young, which carry the dam's genes for size. The size-related ability to produce viable offspring may have been changed by modifications in the environment. Very little is known about how changes in the natural environment for spawning, incubation, and rearing may have contributed to a decline in average size at maturity. Artificial propagation and rearing, such as at Priest Rapids Hatchery, seems to produce adult Brights that are smaller, younger, and more likely to be male than their natural counterparts. The net result is that the average hatchery fish may have only about 0.80 of the reproductive potential of the average natural fish. Changes in growth conditions in the ocean probably did not contribute to the change in size, although the ocean fisheries of Southeast Alaska and British Columbia appear to select, in the genetic sense, against large size and old age in Brights.

Since 1978, in-river commercial fisheries have caught larger Brights and a higher proportion of females than are found in the escapement of the Priest Rapids Hatchery component of the stock, but the fisheries impact the two sexes differently by taking the larger males and the smaller females. The effect on the natural component may differ because of their apparently larger average size. I found no evidence that larger fish or more females were caught when 8-in. minimum restrictions were in effect on gillnet mesh size relative to periods when mesh size was not restricted. Impounding the mainstem during the last 50+ yr may have removed obstacles to migration (e.g., Celilo Falls) that selected for large size in Brights, but that hypothesis could not be tested.

The perserverance of larger and older phenotypes in the Bright stock suggests that countervailing selection -- perhaps during spawning, incubation, and/or early rearing -- may have resisted the

effects of a century of size- and age-selective fisheries. That resistance, however, may reduce the productivity of the stock.

Declines in average size and age at maturity can have undesirable consequences. Lower average size means less biomass landed and lower commercial value. Lower average fecundity and a diminished ability to reproduce in some environments are also expected. Loss of size and age classes may reduce the ability of the stock to adapt to environmental variations.

These results are relevant to several management practices. A holistic approach to fishery management issues is necessary to avoid erroneous conclusions based on narrow perspectives. Measuring reproductive potential of the catch and escapement would be superior to the conventional practice of simply counting numbers of fish. Many aspects of artificial propagation can be improved, including broodstock acquisition, mating regimes, and rearing practices. Stock abundance is a major factor in determining the effect of many management practices on the stock. In general, fisheries managers must be mindful that they manage very complex natural systems.

Changes in Size and Age at Maturity of Columbia River
Upriver Bright Fall Chinook Salmon
(*Oncorhynchus tshawytscha*):
Implications for Stock Fitness, Commercial
Value, and Management

by

Roy E. Beaty

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed February 18, 1992

Commencement June 1992

APPROVED:

Redacted for Privacy

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Date thesis is presented _____ February 18, 1992

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ACKNOWLEDGEMENTS

My sincerest gratitude is extended to the Columbia River Inter-Tribal Fish Commission (CRITFC) for its generous support of this research and my graduate studies. Drs. Jim Hall and Bill Liss proved to be superlative graduate committee co-chairs. Other graduate committee members -- Dr. Roger Petersen (*emeritus*), Dr. Cliff Pereira, and particularly Dr. Phil Mundy -- also contributed substantially to the development of this project. Many thanks to all of them.

Kathryn, my wife, proved not only long-suffering but continually supportive during this project, even when I and the other children were insufferable. She deserves, and receives, my warmest love and appreciation.

Many others, some of whom are cited in the narrative, contributed data, ideas, information, leg work, and other assistance that were essential to the completion of this work. Many of them provided far more than their jobs required, and I hereby acknowledge these contributors:

Charlie Corrarino, Tim Downey, Jim Galbreath (retired), Paul Hirose, Trent Stickell, Ken Bourne, Kirk Beiningen, and Steve Jacobs -- Oregon Department of Fish and Wildlife (ODFW).

N. Kathryn Brigham, B. Paul Lumley, Dr. Howard Schaller (presently of ODFW), Capt. John Johnson, and Mike Matylewich -- Columbia River Inter-Tribal Fish Commission.

Dr. David Hankin -- Humboldt State University

Paul Pedersen and staff at Priest Rapids Hatchery, Paul Wagner, Dale Ward, Susan Markey, Guy Norman, John DeVore, Larry LaVoy (and other staff at the Battle Ground Lab.), Paul Seidel, and Paul Peterson (Cowlitz Hatchery) -- Washington Department of Fisheries.

Keith Hatch -- US Fish and Wildlife Service (presently of CRITFC)

Bill Hart -- (retired) US Geological Survey

Bob Vreeland, R. Z. Smith, George Swan, and Karl Ross
(presently of Don Chapman Consultants inc) -- National
Marine Fisheries Service

Dr. Don Chapman -- Don Chapman Consultants inc.

Duane Neitzel -- Battelle Memorial Institute, Pacific Northwest
Laboratory

Bill Nagy -- US Army Corps of Engineers

Mike Dell -- Public Utility District No. 2 of Grant County

Steven Hays -- Public Utility District No. 1 of Chelan County

Paul Starr -- Canada Department of Fisheries and Oceans

John E. Clark -- Alaska Department of Fish and Game

Larry Brown -- Washington Department of Wildlife

Margaret Haines -- (formerly) Oregon Historical Society

Gary Lundell -- University of Washington Archives

Frederick (Fritz) Cramer, The Dalles, OR; the late Ivan
Donaldson, Stevenson, WA; and Chuck Junge, Redland, OR.

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CHANGES IN SIZE AND AGE AT MATURITY OF COLUMBIA RIVER
UPRIVER BRIGHT FALL CHINOOK SALMON
(*Oncorhynchus tshawytscha*):
IMPLICATIONS FOR STOCK FITNESS, COMMERCIAL
VALUE, AND MANAGEMENT

INTRODUCTION

The Problem

Declines in Size and Age

The average size and age of chinook salmon (*Oncorhynchus tshawytscha*) caught in commercial fisheries along the Pacific Coast of North America have decreased substantially in this century. Troll-caught chinook salmon taken in British Columbia tagging studies of 1949-52 were dramatically smaller and younger than those taken in similar studies during the 1920s (Milne 1957). Between the 1926 and 1949 studies, the modal age of the catch decreased from 4 yr to 3 yr, and age classes 5 and 6 disappeared. At the same time the contribution of fish larger than 19 lb dropped from over 43% to less than 1%. The mean weight of chinook salmon taken in the lower Columbia River (Zone 1) gillnet fishery was significantly lower during 1951-60 than during 1918-40 for all four seasonal fisheries except spring (Pulford 1964). A significant decrease in size also occurred within the period 1951-61 for the same three seasons.

By 1975, catches of chinook salmon by the Washington coastal troll fisheries were markedly younger than during previous periods (Miller 1977). The contribution of age 3 fish to the commercial fishery increased for periods from 1950 to 1975, with concurrent declines in the contributions from older ages. Ages 2 and 3 contributed proportionately more to the sport fishery during 1970-75 than during the earlier period, 1964-69. A shift toward smaller lengths taken in both fisheries reflects the trend toward younger fish in the catch (Miller 1977, Fig. 9 and 10).

Fisheries in British Columbia and Southeast Alaska exhibit a similar trend (Ricker 1980). Average weights of chinook salmon in the British Columbia catch declined by nearly 33% between 1951 and 1975, approximately $0.22 \text{ lb}\cdot\text{yr}^{-1}$. In the Southeast Alaska troll fishery, average weights decreased at a rate of $0.31 \text{ lb}\cdot\text{yr}^{-1}$ from 1960 (17.6 lb) to 1974 (13.3 lb).

After a comprehensive review of size and age trends in chinook salmon catches of the Eastern Pacific Ocean, Ricker (1980) concluded that by 1975, average weights were no more than half of those recorded 50 yr earlier. Even the earliest size and age data that he examined do not represent populations untouched by harvest, as intensive fisheries had operated in some areas for decades prior to the 1920s. Because data from the period prior to heavy exploitation is lacking, the actual magnitudes of declines in size and age since that time may well exceed the estimates of Ricker (1980) and others.

Causes of Declines

Reasons for the declines in size and age of chinook salmon in the fisheries remain unknown, although hypotheses abound. Ricker (1980, 1981) proposed eight possible causes, including the fisheries themselves, environmental changes, and genetic changes. He focused on high exploitation rates by size- and age-selective fisheries as probable agents of genetic changes within and among stocks. Other researchers have supported the same hypothesis (Henry 1971; Van Hying 1973; Schaffer and Elson 1975; Montgomery 1983; Hankin and McKelvey 1985), but there remains some doubt whether fisheries select with sufficient intensity to override natural forces (Healey 1986; Porter et al. 1986; Riddell 1986). The actual causes are so obscure, numerous, and complex that they will probably never be entirely unravelled.

Consequences of Declines

These trends have had obvious adverse impacts on the fisheries. With ceilings on number of fish harvested, fishery revenues are directly related to average weight of the fish caught. Still, the more important long-term potential consequences are less obvious.

Detrimental demographic changes in chinook salmon stocks may be associated with the trends observed in the fisheries. Many theorists argue that the loss of life history types, represented in part by adult size and age classes, may reduce the capacity of a population or species to evolve (Murphy 1968; Schaffer 1974; Helle 1981; Meffe 1986; Hirai 1987). In more immediate terms, if size and age distributions of a population represent adaptive traits (Healey 1986), then anthropogenic changes in those traits could reduce population fitness (Hershberger 1976a; Kapuscinski and Jacobson 1987). Smaller spawners tend to be less fecund (Rounsefell 1957; Mathews and Meekin 1971) and may be less well adapted for reproduction in the native environment (Ricker 1972; Schaffer and Elson 1975; van den Berghe and Gross 1984; Healey and Heard 1984). Less fit spawning populations, which produce fewer recruits, further diminish revenue opportunities in the fisheries.

Despite the great interest and debate regarding declines in size and age in the fisheries, the biology of the individual chinook salmon stocks forming the essential productive foundation of the fisheries has attracted little attention. Have average size and age declined in these stocks? If so, what are the causes and consequences? Examining the problem from a stock dynamics perspective might provide new insights.

Purposes and Overview

This study examined Columbia River upriver bright fall chinook salmon (Brights), a stock closely associated with the problem. Brights are of international interest, making substantial contributions to the ocean fisheries of Southeast Alaska and British

Columbia (Howell et al. 1985a; PSC 1988) and to Columbia River fisheries (ODFW and WDF 1990), in which size and age declines have been documented. The Bright stock was of critical concern during negotiations for the 1985 U.S.-Canada Pacific Salmon Treaty (PST) (Jensen 1986) and is now an indicator stock for monitoring exploitation and escapement during implementation of the PST (PSC 1988). Much production of this stock still occurs naturally (Norman 1984; sources cited in Dauble and Watson 1990), so maintenance of adaptations to the natural freshwater habitat is also important.

Study objectives were to:

- 1) Determine if average Bright size and age at maturity have declined.
- 2) Gain a better understanding of factors that cause changes in size and age at maturity of Brights.
- 3) Describe potential consequences of changes in size and age.

This report is structured around the three study objectives with some additional supporting chapters. Two supporting chapters, which immediately follow, describe the theoretical context of the problem and define the Bright stock. Then the objectives are addressed in turn. Applicable hypotheses, methods, results, discussion, and conclusions are included within appropriate chapters and sections. Concluding chapters describe management considerations and make an overall summary.

THEORETICAL CONTEXT

Evolutionary and related theories provide an essential context in which to consider the significance of changes in size and age at maturity of Brights. These theories will be briefly discussed, and a simple conceptual model of the life cycle will be used to apply theory to the problem.

Evolution, Life Histories, and Adaptive Capacity

Since Darwin (1968, from 1859 original) proposed his "theory of descent with modification", science has sought to better understand the processes of natural selection and evolution. Why do some organisms survive and reproduce while others do not? What traits confer greatest fitness in a given environment, and how must individuals, populations, and species adapt to maintain their fitness in variable environments?

The definition of fitness lies at the very heart of such questions (Stearns 1976). Fitness, according to Stearns (1976, p. 4), is "Something everyone understands but no one can define precisely," but he identifies "fit" organisms as "those better represented in future generations than their relatively unfit competitors." Falconer (1981, p. 301) limits fitness of an individual to "the contribution of genes that makes it to the next generation, or the number of its progeny represented in the next generation," but later (p. 303) he appropriately includes the "quality" of the offspring (F_1) as a component of fitness. Offspring "quality" is presumably their own fitness, which is measured by the number and fitness of their progeny (F_2), whose quality is in turn measured by the number and fitness of their own progeny (F_3), and so forth through subsequent generations ($F_4...$). Hence, the fitness of the original organism (P_1) depends not only on its relative contribution of offspring to the succeeding generation (F_1), but also on its contribution to the population innumerable generations into the future (F_n).

Such a concept of fitness, analogous to Endler's (1986) "durability" and virtually identical to Cooper's (1984) "expected time to extinction", precludes direct measurement because it is a function of uncertain future performances. Only when an organism dies without reproducing is its fitness known (it would have zero fitness). Therefore, fecundity, probability of survival to reproduce, the relative production of viable offspring, and the intrinsic rate of increase are among the commonly used surrogate (or "derived", Cooper [1984]) measures of fitness. These measures will be used as general approximations of fitness in this report. However, the all-important component of long-term persistence must not be forgotten.

A fit organism must adapt to a sequence of environments between conception and death, the pattern of such adaptive changes being known as the organism's life history (Lande 1982). Theorists, drawing heavily upon patterns of mortality and reproduction (for example, Schaffer 1974; Stearns 1976; Stearns and Crandall 1984), attempt to generalize about how life histories relate to the environments in which they occur (Warren and Liss 1980). Stearns (1976) provides an excellent review of life history theory and summarizes the optimum life history strategies that would theoretically be expected under certain environmental conditions.

Common life history patterns are generally presumed to be adaptive, the result of natural selection by prevailing environmental patterns. However, some theorists suggest that some life history traits may be nonadaptive phylogenetic residue (Gould and Lewontin 1979) or merely phenotypic responses to recent environmental changes (Nelson and Soule 1986). Also, mobile organisms have some ability to select their environments, so selection is not a simple unidirectional process from environment to organism. Both adaptive and nonadaptive life history traits no doubt exist, but because current knowledge rarely permits the two types to be differentiated, it seems prudent to assume that prevalent values of life history traits are to some degree adaptive. For example, if the most common age at maturity (a life history trait) is 4 yr (a value of that

trait), then it is likely that maturing at age 4 has been adaptive, relative to maturing at other ages, in the present and past generations.

Environments are spatially and temporally variable to some degree; hence, no single life history type will be optimal in all locales or at all times. Indeed, there is a growing belief that diverse life history types are required for populations and species to adapt, evolve, and persist. This idea is not new; Darwin (1968, p. 163, from 1859 original) recognized the adaptiveness of intraspecific diversity. Recent support comes from theoretical and empirical work at the population and species levels (Van Valen 1965; den Boer 1968; Murphy 1968; Williams 1975; Warren and Liss 1980; Gross 1984; Meffe 1986; Hirai 1987). Although natural selection will favor one life history type (the optimum type) above all others in a particular environment, a population must maintain an array of types to retain its adaptive capacity (Thompson 1951, 1959; Warren and Liss 1980).

The population or species itself -- its abundance, mating habits, etc. -- is an environmental component in natural selection that is easily overlooked despite its possibly preeminent role in the evolution of life history patterns (or strategies, Gross 1987). Competition between closely related individuals or groups, such as for food or mating opportunities, may be a greater arbiter of fitness than physical or other biological environmental components (Darwin 1968, from 1859 original; Gross 1984). Sexual selection, discussed by Darwin (1968, from 1859 original) and Endler (1986), exemplifies interactive processes that can favor traits that might otherwise be maladaptive. Life history patterns must be interpreted in their social as well as their physical context.

To recapitulate: existing life history patterns reflect, at least in part, natural selection associated with certain environments. Intrapopulation and intraspecific interactions may be major fitness-determining components of the environment. Fitness is measured not merely by survival and short-term reproductive performance, but by adaptive capacity -- the ability to adapt and

persist under environmental uncertainty. Adaptive capacity resides in life history and population diversity.

Relevance of Theory to the Study Problem

Differences in size and age at maturity represent some of the differences among life history types of chinook salmon. These differences may in turn represent adaptations to different environments (Warren and Liss 1980; Healey 1986; Nicholas and Hankin 1988).

The relationship between life history types and the sequential environments of anadromous chinook salmon life-cycles can be illustrated with a simple graphic model (Fig. 1). Consider the continuous sequence of environments as series of discrete events, with each event associated with a simplified developmental states: incubation, early rearing in fresh water, downstream migration, ocean rearing, spawning migration, and spawning. Within each developmental environment, limiting factors constrain chinook salmon to a window of opportunity that permits continued development. The relatively few fish that successfully negotiate all windows survive to reproduce, and the various patterns of their adaptations constitute successful life histories. To the extent that the adaptations are heritable (see p. 43, Heritability of Size and Age at Maturity), the successful life history types will be represented in the next generation. If the windows of opportunity are similar for the next generation, then those offspring inheriting previously successful adaptations will be favored, and selection for optimum life history types will continue.

Developmental environments influence size and age at maturity in at least four principal ways: (1) selecting optimal sizes and ages for spawning migration and spawning (direct selection), (2) selecting traits for other developmental environments that are correlated with size and age at maturity (indirect selection), (3) inducing purely phenotypic responses that do not change the relative fitnesses of size and age genotypes, and (4) reducing effective population size and thereby increasing the frequency of random genetic events.

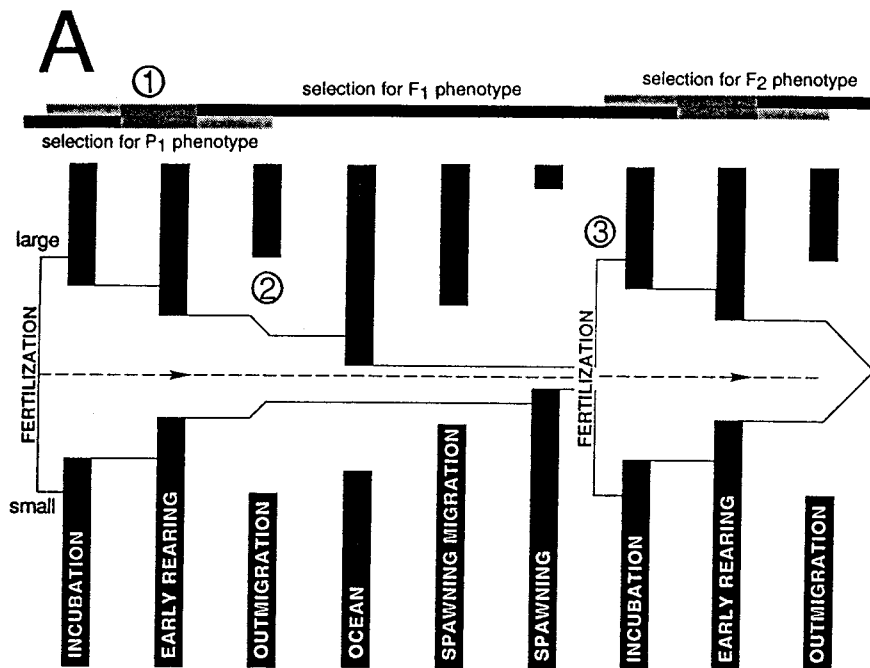


Figure 1. Selection by environmental "windows" and other possible reasons for change in size at maturity of Brights. Each generation begins at fertilization with the genetic potential for a range, from large to small, of sizes at maturity. As individuals of the generation develop, the various environments may select against particular sizes at maturity either directly -- as during the spawning migration and spawning, when the traits are expressed -- or indirectly by acting on correlated traits. Vertical bars represent simplified environments; vertical distance between the solid horizontal lines represents the range of potential sizes and, in some cases, numerical abundance of individuals. Dashed lines show range mid-points at relevant periods in the life cycle. Truncation selection is shown for simplicity, although environmental windows would not select so sharply on a quantitative trait like size at maturity. Note that selection may operate continually as the population flows from generation to generation, but the results are observable only during the spawning migrations and spawnings of each generation.

- A. Because the size of the female parent greatly influences the phenotype of the progeny during their early life stages (see *Maternal Influences*, p. 50), selection on maternal size continues into the filial generation (1). The outmigration environment (2) may not be selective for adult size (hence the broad window), but a narrowing of the band represents a reduction in numbers due to high mortalities. At fertilization (3), genetic recombination regenerates a range of potential sizes at maturity, centered on the average parental size, in the next generation.

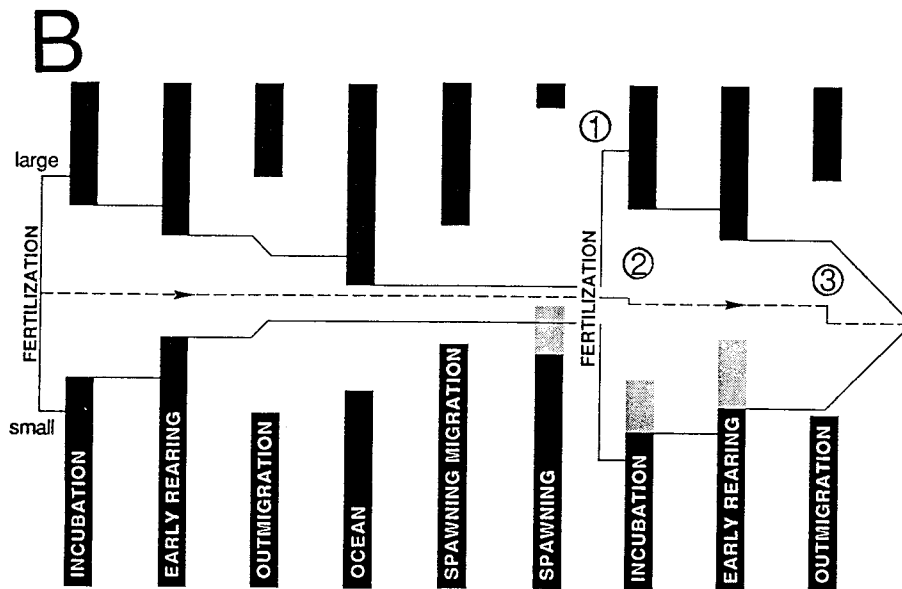


Figure 1. (continued)

B. Reduced size at maturity may result from relaxed selection against small size in some of the environments. In this example, selection is relaxed (shaded portion of bars) in the spawning, incubation, and early rearing environments, as might occur with artificial propagation. Because more adults spawn successfully, more embryos may result and represent a broader range of potential sizes at maturity (1). The reduction in selection at spawning causes a small decrease in the average potential size at maturity (2). Reductions in the selectivity of the incubation and early rearing environments could contribute to a further decrease in average size (3), if not counteracted in later environments.

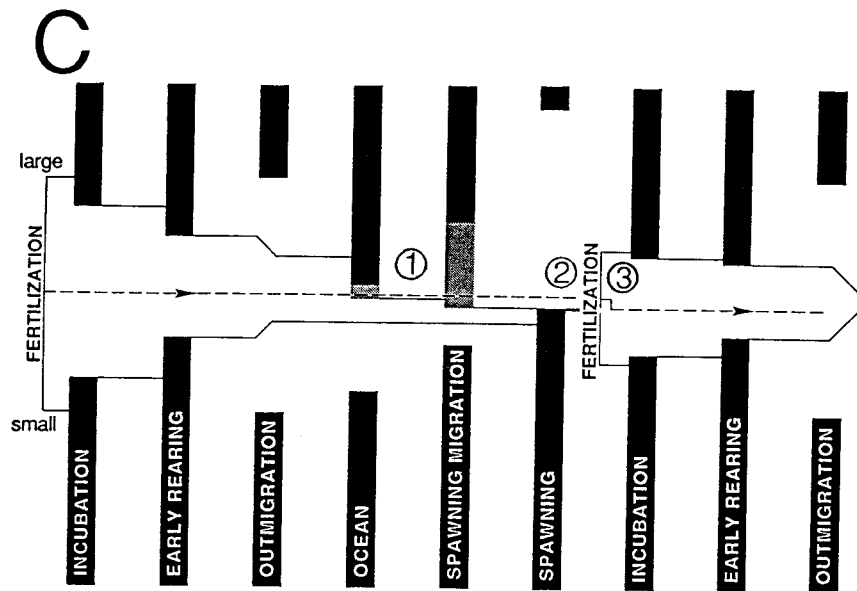


Figure 1. (continued)

C. Increased selection against large size (shaded portions of bars) could cause a reduction in size at maturity. Ocean and in-river fishing are examples of such selection in these environments (1). Selection against small size at spawning could counteract this change, but the combined result is a very small effective spawning population (2). Random genetic events may cause changes to any and all traits at low effective population sizes. The reduced reproductive ability of the escapement results in fewer offspring per spawner, although the average potential size at maturity in the next generation is little changed (3).

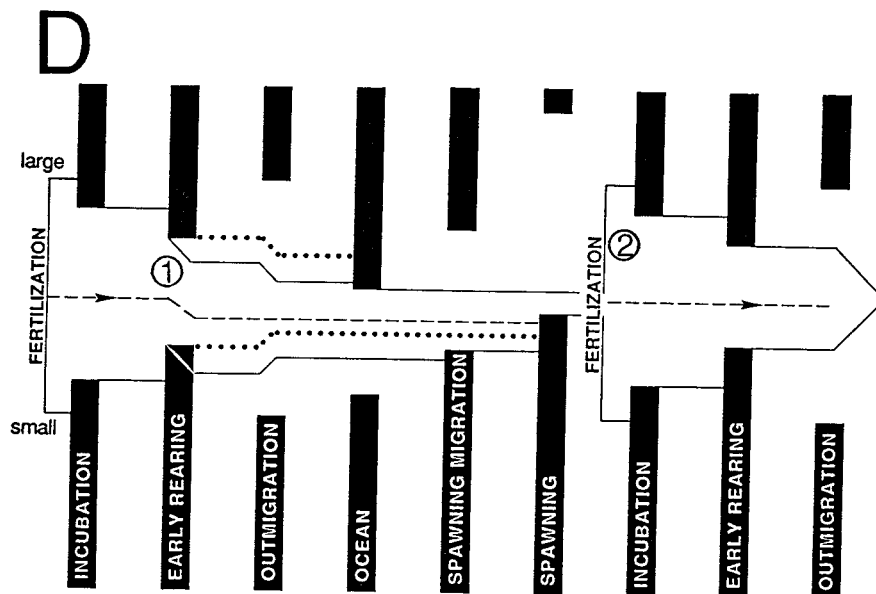


Figure 1. (continued)

D. Environmental conditions may alter the expression of the genetic potential. This example illustrates a shift to smaller potential average size at maturity caused by superior growth during early rearing (1). Dotted lines represent the range that would have been impacted by environmental windows had the shift not occurred. With the shift, fewer potentially large fish are selected out by the ocean environment, and more of the smaller and intermediate genotypes are selected out, because of their smaller phenotypes, during the spawning migration and spawning. The net result may be little change in the genetic potential for size at maturity in the next generation (2) or possibly a change favoring genotypes for larger size, due to the greater selection in the spawning migration and spawning environments.

Hypotheses relating the adaptiveness of size and age traits to migrational and spawning environments are common (for example, Hanson and Smith 1967; Schaffer and Elson 1975; Chebanov 1980; van den Berghe and Gross 1984; Hankin and McKelvey 1985; Healey 1986; Holtby and Healey 1986). However, prevalent values of these traits are not necessarily genetically programmed optima for migration and spawning (Miller 1957; Healey 1986; Nelson and Soule 1986). Size and age at maturity may be correlated with other heritable traits (e.g., growth rate) that are adaptive or maladaptive for other developmental environments. If so, size and age distributions in the spawning run may reflect compromises among heritable adaptations for several developmental environments (i.e., counteracting selection). In addition to selecting in favor of heritable size and age adaptations, environments could have only phenotypic effects on the traits, such as when superior growth conditions prompt anomalously early maturation (Riddell 1986). Random genetic events can disrupt adapted gene complexes during population bottlenecks when spawning numbers are severely restricted or mating patterns are distorted (Kapusinski and Jacobson 1987).

Shifts in distributions of size and age at maturity can reflect environmental changes that are either beneficial or detrimental for the population. For example, relaxed selection against small size that results in smaller mean sizes can also promote increased survival and production (a benefit) if the relaxed selection is not counteracted in another environment (Fig. 1.B). In this case, reduction in size may lead to, and result from genetic adaptation to a modified environment (e.g., one in which smaller fish are preyed upon at a lower rate than formerly), a process necessary for the long-term survival of the population. Similarly, improved growth conditions may benefit survival while depressing mean age (and size) at maturity (Fig. 1.D). As an example of a detrimental environmental change that results in smaller average size, consider intensified selection against large size (e.g., in a fishery), which may result in counteracting selection that is strong enough to nearly extinguish the population (Fig. 1.C). Without some knowledge of the causes, or

the associated changes in survival or production, the implications of shifts in size or age structure cannot be clearly interpreted as either beneficial or detrimental to the population. Generally, however, any reduction in the range of sizes and ages at maturity represents a loss of life history types, hence a reduction in adaptive capacity. Life history diversity confers adaptability under changing environmental conditions.

Observed values of size and age at maturity of chinook salmon are probably adaptive for the unique sequences of environments encountered during their life cycle. Changes in size and age at maturity probably reflect environmental changes, although the mechanisms are numerous and complex.

WHAT IS A BRIGHT?

A basic knowledge of the phylogenetic, geographic, and historical context of Brights is required to understand the significance of present life history patterns such as size and age at maturity. This chapter summarizes that context and defines the Bright stock.

The Bright Family Tree

Bright ancestors have demonstrated great adaptability. Adaptation to marine rearing environments, perhaps by a *Salmo*-like ancestor (Neave 1958; Hoar 1976; Miller and Brannon 1982; Smith and Stearley 1989; but see Thorpe 1982), allowed the development of anadromy and the eventual extension of spawning ranges into streams throughout the northern hemisphere. Pacific salmon (*Oncorhynchus* spp.) may have arisen in brackish waters from an ancestor resembling their recently reclassified congeners, Pacific trout (Neave 1958; Smith and Stearley 1987). Facultative anadromy and isolation by Pleistocene glaciation (Neave 1958; Allendorf and Thorgaard 1984), differing temperature regimes (Miller and Brannon 1982), and behavioral barriers (Neave 1958) have probably contributed to the radiation of at least eight species (Smith and Stearley 1987) and perhaps tens of thousands of stocks (Ricker 1972) within an evolutionarily brief time (Neave 1958).

Within its genus, *O. tshawytscha* is considered intermediate in evolutionary advancement (Neave 1958; Hoar 1976; Miller and Brannon 1982). It displays increased specialization for marine life (Wagner et al. 1969), considered an advanced trait (Neave 1958; Hoar 1976), but still retains vestiges of "primitive" facultative anadromy (Merrick 1984; Stokell 1955; Brown 1984) and iteroparity (Rich 1922; Gebhards 1960; Robertson 1957; see also possible evidence in Swartzell 1967). Such a diverse life history repertoire may have enabled the chinook salmon to colonize its broad native spawning range, which spanned from California's San Joaquin River (Fry 1961)

around the North Pacific and Bering Sea to perhaps Hokkaido, Japan (O'Malley 1920), and to survive major habitat perturbations within its range.

In the Columbia River, where much of the indigenous fish fauna is euryhaline or anadromous, anadromy may have been an important adaptation for recolonizing habitat often disrupted by large-scale geologic events (Li et al. 1987). Aboriginal peoples on the Columbia used salmon at least as early as 10,000 yr ago (NPPC 1986), so salmonids may have inhabited the Columbia River Basin during the late Pleistocene when repeated failure of glacial dams unleashed the cataclysmic Bretz, or Spokane, Floods (McKee 1972; Allen et al. 1986). In more recent centuries the lower river was dammed by a massive landslide (ca. 1250 A.D.; Lawrence and Lawrence 1958) and thickened with ash from volcanic eruptions (Dawley et al. 1986). Chinook salmon stocks have had to remain adaptable to survive in the Columbia Basin.

Recent Historical Context

Dramatic geologic events did not prevent the Columbia River from becoming perhaps the world's greatest producer of chinook salmon (Ricker 1972), but overharvest and exploitation of other river resources by Euroamericans have greatly reduced the Columbia's salmonid populations (NPPC 1986). Predevelopment runs of 4.8 million to 9.2 million chinook salmon have dwindled to only 1.6 million in recent years (NPPC 1986, Table 6), of which probably fewer than half are produced naturally. Fisheries, river developments, and artificial propagation are major anthropogenic environmental disruptions that probably have induced changes in Bright life history patterns.

Fisheries

The salmon resources of the Columbia Basin have long sustained its human inhabitants. Aboriginal peoples may have harvested over

one million Columbia River chinook salmon annually before diseases decimated the native human populations in the 1700s and early 1800s (NPPC 1986). Euroamericans began commercial exploitation as early as the 1820s and 1830s (Craig and Hacker 1940; Smith 1979), but not until after the onset of the canning industry in 1866 (Collins 1892) were the salmon runs heavily exploited. Large, bright, oil-rich spring- and summer-migrating chinook salmon were the foundation of the commercial fishery and processing industry (Smith 1895; Rich 1942; Thompson 1951). Only 17 yr after the inception of the canning industry (i.e., in 1883) at least 39 canneries (Craig and Hacker 1940; Smith 1979) were packing catches of approximately 2.3 million fish (over 40 million lb; Fig. 2; NPPC 1986). In addition to these enormous packs, many tons of chinook salmon were discarded when packing capacity was exceeded (Cobb 1911).

The unbridled exploitation in the lower river took its toll on the stocks. Chinook salmon of the spring and summer runs, although abundant in upper reaches of the Columbia and Snake Rivers during the 1870s, were scarce in the same areas by 1890 (Gilbert and Evermann 1895). By that time "the river was literally filled with devices for the capture of salmon," (Collins 1892, p. 221), and overfishing was generally acknowledged as fact (Smith 1895). However, increasing effort (Smith 1895) and increasing contributions from less desirable fall-run chinook salmon (Rich 1925; Fulton 1968) maintained relatively high but variable harvests through at least 1920 (Fig. 2) (Rich 1940b; Van Hyning 1973; Smith 1979). By 1919, the August (fall) run was "overwhelming in importance," (Thompson 1951 p. 24) and in the 1940s Brights and other fall-run chinook salmon were making the major contribution to in-river fisheries (Van Hyning 1973). Estimated harvest rates of fall chinook salmon in the "lower river" (probably the reach below the present site of Bonneville Dam) for 1928-54 range from 54% to 89% (excluding 37% during a fishermen's strike in 1952; Gangmark 1957). These estimates may be conservative (Van Hyning 1973).

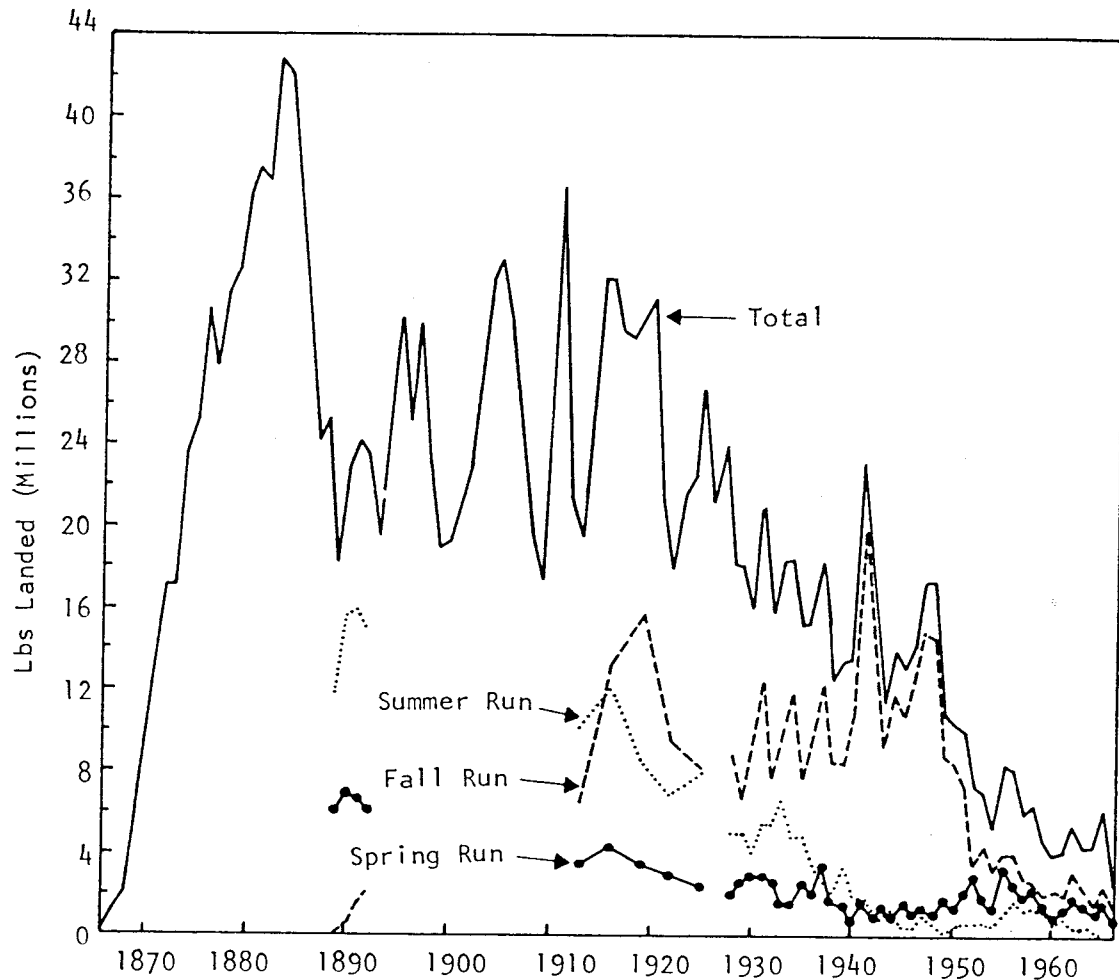


Figure 2. Chinook salmon landings, by run, in the Columbia River commercial fishery, 1866-1966. From Van Hyning (1973).

Sizeable harvests probably were also occurring outside the river; ocean fisheries as far north as Alaska take Brights and other Columbia River fall chinook salmon. The Southeast Alaska troll fishery, begun in 1905 (Cobb 1911) and with a peak chinook salmon catch of 17 million lb (approximately 0.9 million fish) in 1937 (Parker and Kirkness 1956), is known to harvest large numbers of Brights (Funk 1981; PSC 1988). The British Columbia troll fishery began before 1910 (Rounsefell and Kelez 1938) and as early as the 1920s was known to be taking many Columbia River fall chinook salmon (Williamson 1927). Net fisheries have been restricted to the inside

waters of both the United States and Canada since the mid-1950s (Royce 1988), but they likewise catch Brights (Howell et al. 1985a; PSC 1988). Increased catches in the ocean fisheries between Oregon and British Columbia have been implicated in the reduced run sizes of fall chinook salmon of the late 1940s to the early 1960s in the Columbia River (Van Hyning 1973). Over 83% of the 1974-77 brood Brights that were harvested were taken in Southeast Alaska and British Columbia (Howell et al. 1985a, p. 411), and Brights may have been the principal support of commercial ocean fisheries in these areas in some more recent years (PSC 1988).

For most of a century, in-river and ocean fisheries have been harvesting Brights. Hence, the size and age distributions previously and presently observed in the stock may be in part an artifact of intensive and selective exploitation. During the same period the stock's freshwater habitat has been radically altered.

Development of the Columbia River

Since Euroamerican occupation of the Columbia River Basin, its water has been put to almost every conceivable use. Perhaps without exception those uses have promoted environmental changes to which salmon populations have had to adapt. Craig and Hacker (1940), Fulton (1968), and NPPC (1986) provide sobering reviews of the impacts that agriculture, logging, mining, nuclear reactors, and other developments have had on salmon habitat.

Dams probably have had the most profound influence on Brights. Over 140 hydroelectric, multipurpose hydroelectric, and irrigation dams exist in the basin (NPPC 1986). Beginning in 1931 with the completion of Rock Island Dam on the mid-Columbia, the mainstem spawning and rearing habitat of Brights has all but been eliminated by dams and reservoirs (Fulton 1968; NPPC 1986). Additionally, mainstem dams and reservoirs are known to delay adult and juvenile migrations (Schoning and Johnson 1956; Raymond 1969), trap sediments and reduce turbidity that once may have cloaked vulnerable migrating juvenile salmonids (Junge and Oakley 1966), harbor large populations

of indigenous and exotic predators (Poe and Rieman 1988), kill substantial numbers of juveniles that pass dams (Schoeneman et al. 1961; review and annotated bibliography in Burchfield et al. 1986), and enable radical alteration of flows in unimpounded reaches (Becker 1985; Chapman et al. 1986). Li et al. (1987) provide additional examples of impacts.

Large storage reservoirs such as Lake Roosevelt behind Grand Coulee Dam have caused other environmental changes that, although subtle, may be serious. For example, Lake Roosevelt slightly increases and dampens the variability of river temperature and delays the annual temperature cycle by approximately 30 days (Jaske and Goebel 1967). If spawning, incubation, and early rearing success are dependent on a time-temperature match, the filling of Lake Roosevelt in 1941 would have substantially shifted the optimum spawning time for chinook salmon (e.g., Brights) in the mainstem waters downstream of Grand Coulee Dam. Present-day Brights may be descendents of individuals that were able to adapt during the last 50 yr to this temperature shift.

Like the fisheries, development of the Columbia River has changed the environmental windows of opportunity for spawning, incubation, and rearing, which may influence adaptive sizes and ages at maturity. Not only what we observe now, but also the earliest size and age data available, could have been influenced by these shifts. Another environmental change of great significance is the use of hatcheries to replace natural spawning and rearing habitat and mold the patterns of production to enhance fisheries.

Artificial Propagation

Artificial propagation has long been the management answer to overfishing and habitat destruction. It can affect Bright size and age at maturity through two principal means: 1) changing the species and stock composition in the runs in ways that alter the competitive environment and the prosecution of fisheries, and 2) subjecting the cultured stocks to different selective environments than would occur

with natural production. (The latter is discussed in detail under Early Rearing, p. 50.)

The first hatchery in the Columbia River Basin was built in 1876 (Wahle and Smith 1979) or 1877 (Smith 1979) by a private firm on Oregon's Clackamas River, which joins the Willamette not far from its confluence with the Columbia. This hatchery was operated sporadically (1887 was the only year during the 1880s) and released only chinook salmon fry¹ (Wahle and Smith 1979), yet was credited with producing the increased run of 1890: "It is believed by those competent to judge that this [improved run] is directly traceable to artificial propagation at the hatchery on the Clackamas," (Collins 1892). By 1894 "practically unanimous" faith was being placed on artificial propagation to regenerate the fishery (Smith 1895 p. 241). Between 1895 and 1900 construction was completed or begun on at least seven additional salmon hatcheries on Columbia River tributaries, all emphasizing release of chinook salmon fry (Wahle and Smith 1979).

The Mitchell Act of 1938, intended to compensate for habitat destruction by water use projects in the Columbia River Basin, initiated the next major period of hatchery construction (Wahle and Smith 1979). Although upriver stocks suffered most from water use projects, all but one rearing pond (Ringold) of the 22 hatcheries and three major rearing ponds built with Mitchell Act funds since 1949 were sited on the mainstem or tributaries below McNary Dam (NPPC 1986). Of the 82 anadromous fish hatcheries and rearing ponds operated in the Columbia River Basin between 1960 and 1976, 49 (60%) were below McNary Dam and 28 (57%) of those 49 produced fall chinook salmon (fall chinook salmon were a minor group in 6 of the 28; Wahle and Smith 1979, data from Tables 14, 17, and 19). By the 1970s, hatcheries were producing over 70% of the fall chinook salmon outmigrants; hatchery releases of fall chinook salmon in the Columbia River approached 100 million juveniles by the early 1980s (Bottom et al. 1984; NPPC 1986). The resulting flood of mostly dark, or "tule",

¹ Even with modern technology, unfed chinook salmon fry released from hatcheries are believed to survive at very low rates (sources cited in Miller et al. 1990 and Steward and Bjornn 1990).

race fall chinook salmon in the lower river has promoted overharvest of the natural upriver stocks (Brights), whose migration time coincides with that of the tules (NPPC 1986).

Spawning channels were employed in the 1960s and early 1970s to mitigate for destruction of Bright spawning habitat by mid-Columbia dams (those between Grand Coulee Dam and the confluence with the Snake River; Fig. 3). Designed to enhance survival in a seminatural spawning, incubation, and rearing environment, the facilities were plagued by high mortalities and poor returns (Chambers et al. 1963; Allen and Moser 1967, 1968; Allen and Meekin 1973). The concept was abandoned during the 1970s, and the facilities were converted to conventional tray incubation and raceway culture. Spawning channels were a laudable attempt to maintain a selectively natural freshwater environment and provide in-place and in-kind mitigation.

Artificial propagation has been embraced as the remedy for overharvest and habitat destruction, but its focus has been the expeditious enhancement of harvests, not the mitigation of damage to depleted stocks. Brights have not only adapted to environmental changes wrought by large-scale production of tule fall chinook salmon in downstream hatcheries, but are themselves increasingly being exposed to the hatchery environment. How hatchery practices influence size and age at maturity will be considered in later chapters; first let us define the Bright stock.

The Bright Stock

The term, "stock," has no explicit, universally accepted definition (see Howell et al. 1985a for discussion). In purest form, a stock is a population (or subpopulation, Nelson and Soule 1987), an interbreeding or potentially interbreeding group of individuals (Hershberger 1976a). In practice, a stock is a management unit of a species distinguished from other such units by differences that (1) are presumably based on genetic differences, (2) are readily

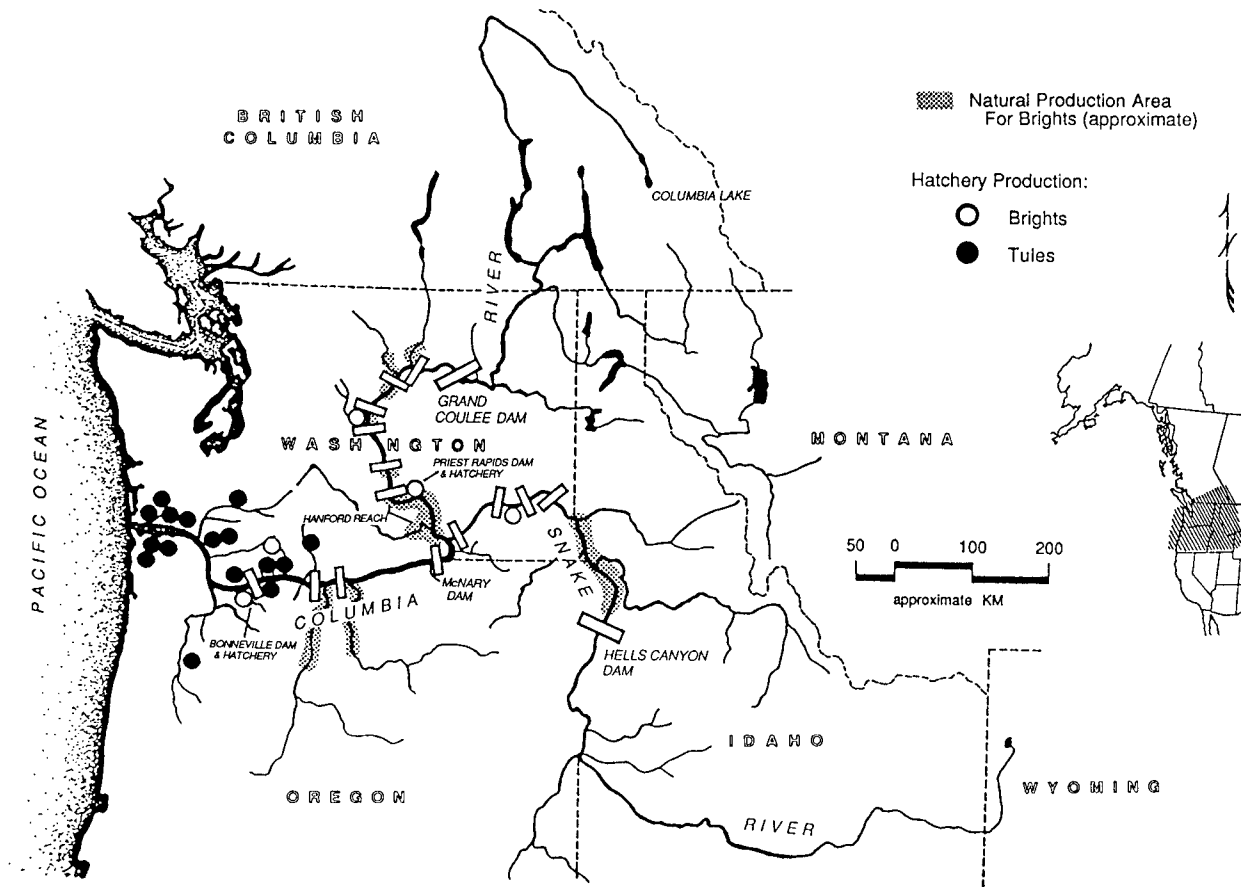


Figure 3. Present production areas of fall chinook salmon in the Columbia River Basin. Tule natural production not shown; use of some spawning areas by Brights was documented only during recent high escapements. Data from Howell et al. 1985a; Kohn 1988; Rogers et al. 1988; Heindl and Beaty 1989; and S. Hays., Chelan County Public Utility District, Wenatchee, WA, pers. comm. 1/89.

measurable, and (3) do not result in groupings that are impossible or unduly inconvenient to manage.

Brights are a heterogeneous group of fall-running chinook salmon that, along with their progenitors, have demonstrated their ability to adapt to severe anthropogenic environmental changes in the past 100+ yr. These human-caused changes are great enough to have created Brights as a relatively distinct stock, so early data on "Brights" must be used with care and proper qualification.

Brights are a fall-run stock, which under the current definition means that they pass Bonneville Dam on or after August 1. Columbia River fishery managers recognize four fall stocks, Lower River Wild, Lower River Hatchery, Bonneville Pool Hatchery, and Brights (Howell et al. 1985a). Bonneville Dam separates the lower and upper river stocks under this classification. Lower River Hatchery and Bonneville Pool Hatchery stocks are tules that return to the river when very ripe and spawn after little delay.

The spawning distribution of fall chinook salmon is a fragmented vestige of its former extent (Fig. 3 and 4). Natural Bright production has been replaced by production of tule fall chinook salmon in the lower river and Bonneville Pool, and to a lesser extent by Bright hatchery production in both lower and upper areas. Upper Columbia River wild Brights, depressed in the 1970s, were considered for listing as a threatened or endangered species under the Endangered Species Act (Horner and Bjornn 1979). However, the stock rebounded in the late 1980s, but is presently in decline (Fig. 5). Brights from all sources have contributed between approximately one-quarter and one-half of adult fall chinook salmon in the Columbia River since 1980 (Fig. 6).

The Bright stock is a complex unit (Howell et al. 1985a). The primary substock originates from natural (in the Hanford Reach) and hatchery (mostly Priest Rapids Hatchery) production between McNary and Priest Rapids Dam (Fig. 3). Several minor components include natural production in the Snake, Deschutes, and other tributary rivers above The Dalles Dam as well as hatchery production in the lower and upper river.

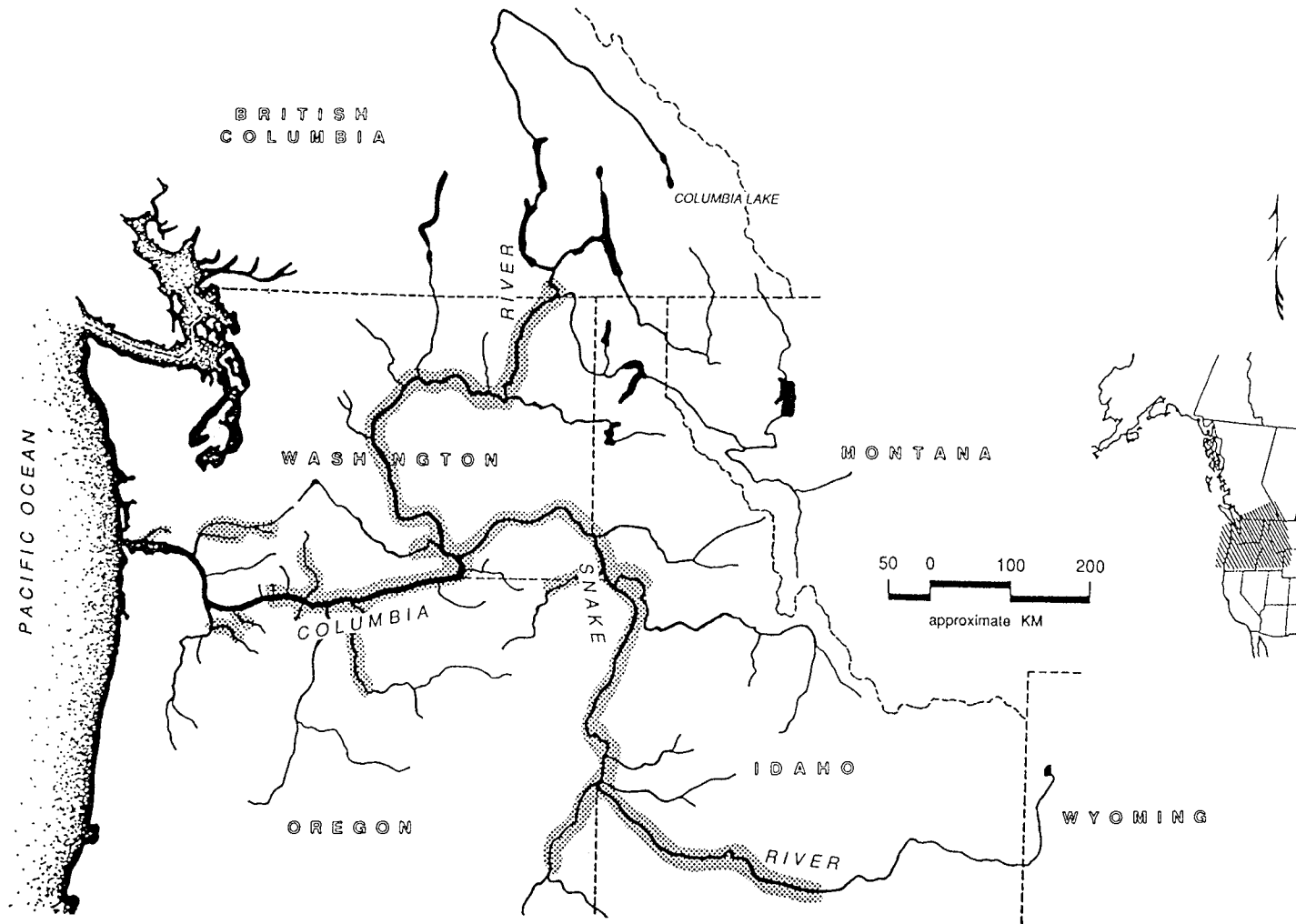


Figure 4. Estimated former extent of fall chinook salmon spawning in the Columbia River Basin (adapted from Fulton 1968).

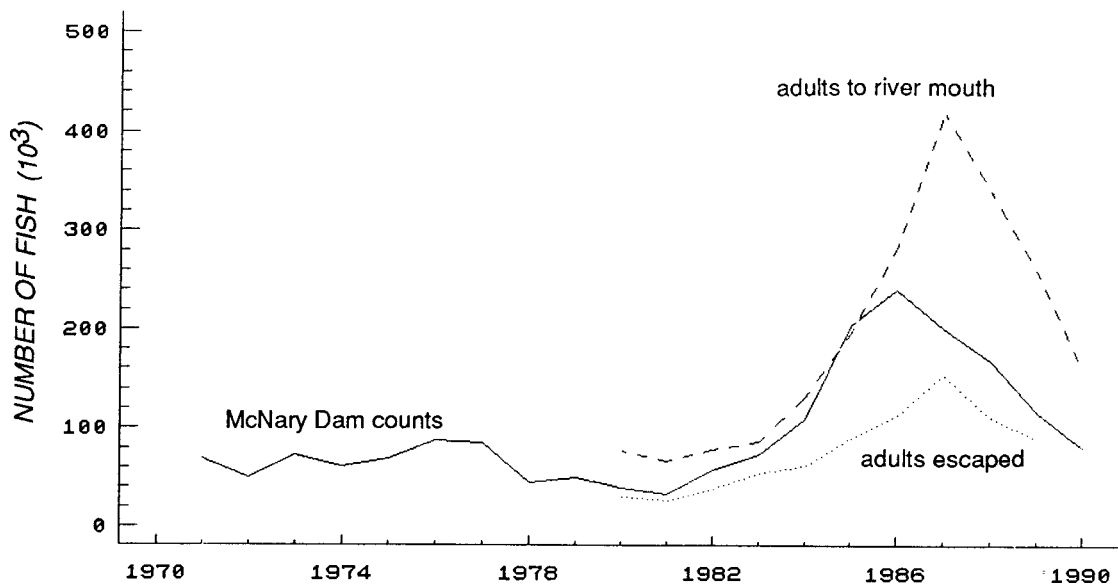


Figure 5. Bright run sizes and escapements. Counts of fall chinook (adults and jacks, combined) at McNary Dam from USACE (1989) and the Columbia River Inter-Tribal Fish Commission, Portland, OR (unpubl. data, B. P. Lumley). Estimated adult run size from ODFW and WDF (1990) (years 1980-89) and from Washington and Oregon Columbia River Staff (Dec. 5, 1990, memo to Columbia River and Ocean Salmon Managers, preliminary accountability of the 1990 return). Adult escapement estimates are from ODFW and WDF (1990).

Differences between subunits suggest that the present Bright stock comprises more than one population (Horner and Bjornn 1979; Utter et al. 1982, 1987; Seidel et al. 1988). Although Horner and Bjornn (1979) considered the stock to be relatively "pure" of exotic genetic material, it is quite likely that trapping Brights for hatchery brood stock at downstream dams and transferring eggs and juveniles around the Bright production area has been eroding the genetic differences between Bright populations and may be disrupting gene complexes that are adaptive for particular streams and areas.

This study examines the primary substock, which is produced naturally in the Hanford Reach and artificially at Priest Rapids

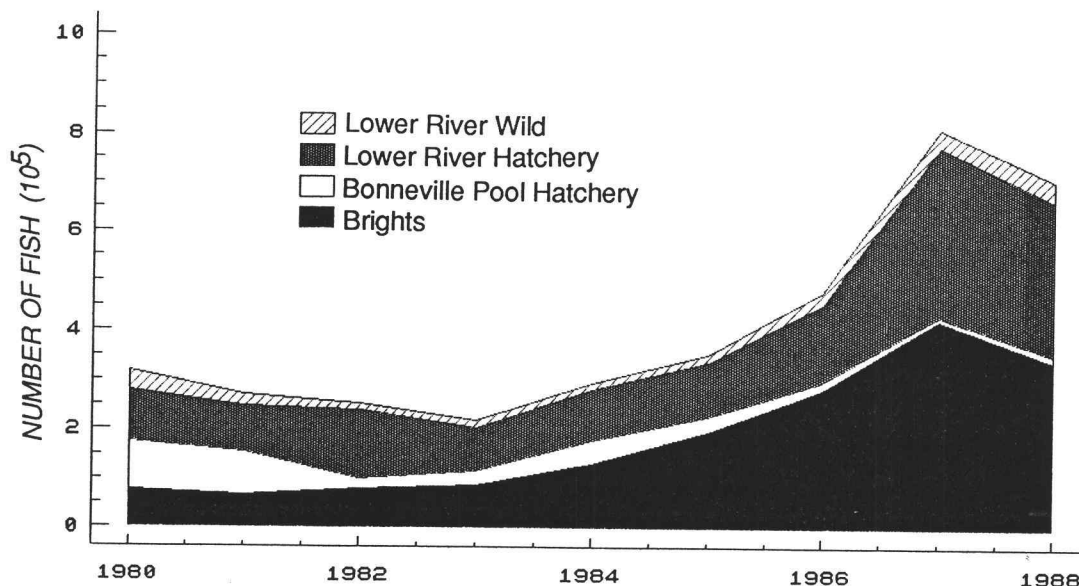


Figure 6. Estimated stock composition of the fall chinook salmon run (adults only) to the mouth of the Columbia River, 1980-88. From data in ODFW and WDF (1989).

Hatchery. Subsequently, "Brights" will refer to this substock unless noted otherwise.

Brights are probably different now than historically. Seufert (1980, p. 7) reports that:

In the 1920s there were almost no Chinook salmon at The Dalles during the fall seasons that started on September 10. Some years there was not one single Chinook caught at The Dalles, and when any were taken at The Dalles it was a rarity. It was not until 1933 that the big fall Chinook run showed up on the Upper Columbia River. Why they came then, or from where, no one knows. Everyone was taken completely by surprise.

However, Delbert Frank, Sr. (Warm Springs, OR., pers. comm. 8/21/90), a tribal fisherman who began fishing at Celilo Falls in 1927, recalls a strong fall chinook salmon run coinciding with the coho salmon run even before 1933. Other tribal fishers who began fishing a few years later at Celilo say that their parents and other elder fishers never

mentioned the sudden appearance of the fall run of chinook salmon at Celilo (Levi George, Sr. (deceased), and Wilferd Yallup, Toppenish, WA, pers. comm. 7/30/90). The presence of migrating adult chinook salmon at Kettle Falls (on the mainstem Columbia River just below the border with Canada) through November in the 1890s demonstrates the existence of an upriver, fall-spawning stock at that time (Gilbert and Evermann 1895). Brights spawn primarily in November, the latest of present chinook salmon stocks in the Columbia River. It may be that during the 1920s and early 1930s Brights were growing in numbers and emerging as a distinct stock.

Rather than discrete runs or stocks, the chinook salmon in the Columbia to some extent may have formerly composed a cline distributed through a relatively continuous spatial-temporal-thermal habitat spectrum (see Thompson 1951; Miller and Brannon 1982; Mullan 1987). Similarities between Brights and summer chinook salmon (Schreck et al. 1986), suggest that these two stocks may be essentially the same except for occupying slightly different positions on the spatial-temporal-thermal spectrum. Thompson (1951) suggested that the Bright stock, which is now relatively distinct, emerged from the late tail of the summer run that was protected for many years by an in-river fishery closure. Timing of the Bright run corresponded well with the time of this closure (Thompson 1951), which was August 10-September 10 in 1890 and reduced to August 25-September 10 by 1905 (Wendler 1966). Given the heritability of time of migration, it is probably no coincidence that a great majority of the fall run still passes Bonneville Dam during these days of late summer (Fig. 7). Habitat that was underseeded due to high exploitation rates on other stocks may have facilitated rapid growth of the Bright stock. The present identity of Brights appears to be at least partially a result of intensive and selective fisheries; habitat destruction, fragmentation, and modification; and stock management practices during the last century (Thompson 1951; Becker 1970; Watson 1970; Mullan 1987).

In summary, Columbia River chinook salmon descend from a very adaptable line. Brights have demonstrated their ability to adapt to

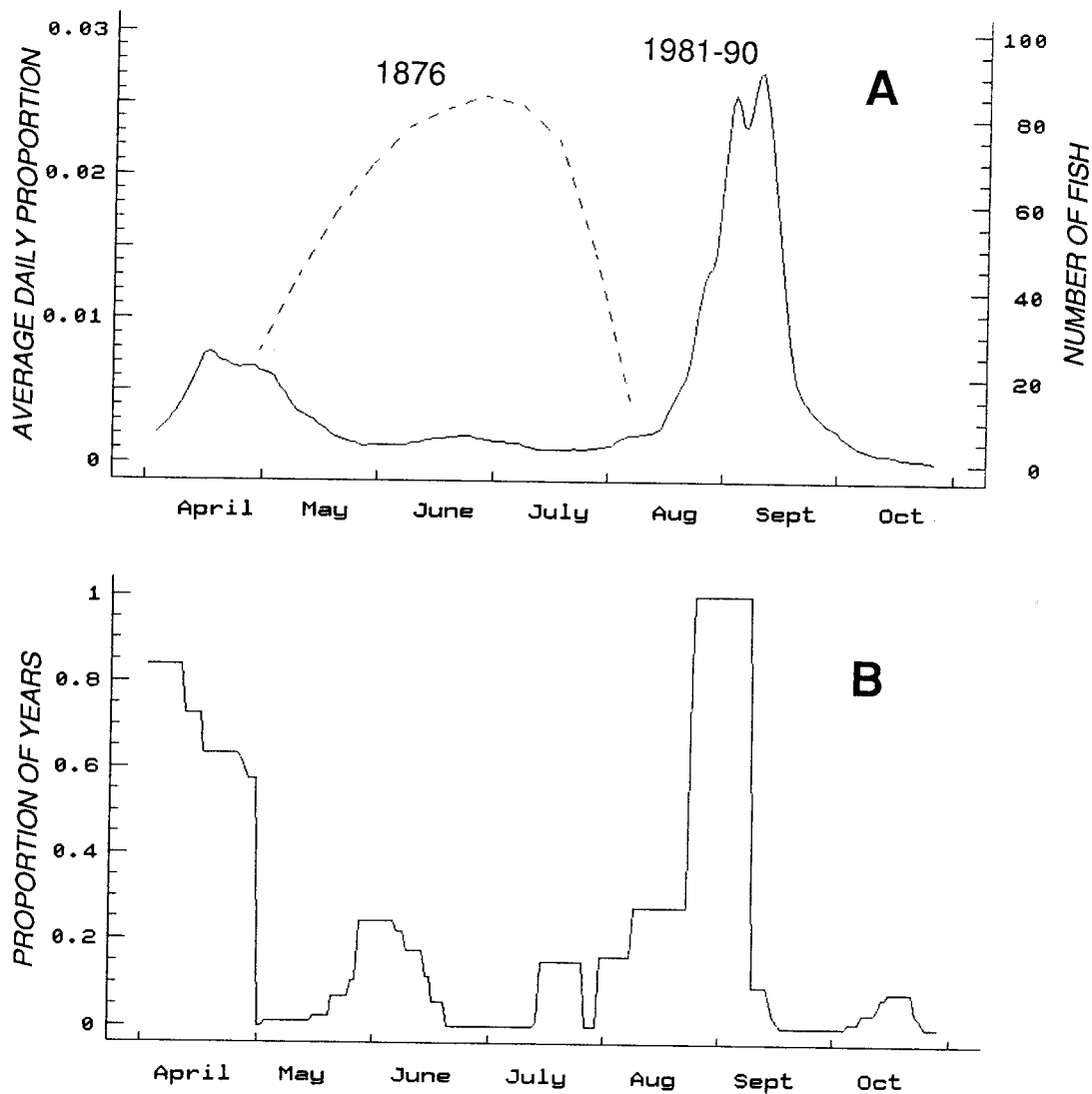


Figure 7. Comparison of recent and historical run timing of Columbia River chinook salmon (A) and historical closures of the in-river commercial fisheries (B).

- A. Data for 1876 are daily catches of chinook salmon per gillnet boat delivering to a cannery in Astoria, OR, derived by smoothing (by eye) Figure 6 in Thompson (1951). Curve for 1981-90 is 5-d moving average of daily proportion of total annual counts of adults at Bonneville Dam (data from B. P. Lumley, Columbia River Inter-Tribal Fish Commission, Portland, OR).
- B. Proportion of years from 1877 through 1963 when commercial salmon fishing in the Columbia River was closed by both Oregon and Washington on each day from April through October. Data adapted from Wendler (1966, Table 3 and Figure 4).

major environmental changes in the last 100+ yr, changes that may have caused Brights to emerge as a distinct, although heterogeneous, stock. Historical data must be carefully examined and qualified in the context of these changes in Brights and their environment before such data can be considered representative of this stock.

CHANGES IN BRIGHT SIZE AND AGE AT MATURITY

The first study objective, to determine if average Bright size and age at maturity have declined, will be addressed in this chapter. The null hypothesis is that mean size and age in the Bright spawning run are the same in recent as in earlier years.

Methods

Published and unpublished sources were searched for historical Bright size and age data. I found no data from the virgin stock (i.e., prior to ca. 1890), and references to average size dating from the period of accelerating fall chinook salmon harvests (1890-1920) are little more than anecdotal generalizations (Appendix A). Hence, the stock was probably heavily exploited (and perhaps altered) before size data were collected.

Catches in the in-river fisheries are the primary sources of size data. Season and location of the catch were used to identify data with a higher likelihood of representing Brights. Cannery records of deliveries from August trap catches near the river's mouth between 1918 and 1934 (Chapman 1940) provide early points, estimates from on-site sampling by biologists and fish purchase receipts ("fish tickets") for dipnet catches at Celilo Falls during or after mid-September between 1949 and 1956 provide intermediate points, and recent years (1980-86) are represented by fish ticket data from commercial gillnet catches in The Dalles and John Day pools (compiled from data in annual Washington Salmon Landings, Washington Department of Fisheries [WDF], Olympia, WA). All of these estimates are probably biased by gear selectivity, prior downstream removals by selective fisheries, or the presence of other stocks in the sample, but they are the most representative data that I could obtain. Data validity will be further considered in the discussion; used and unused data are described in Appendix A.

Recoveries in the in-river fisheries of binary coded wire tagged (CWT) Brights originating from Priest Rapids Hatchery and

scale ages of samples from escapement areas are the basis of annual estimates of numbers of fish by age for Bright runs to the river in 1980-86 (unpublished data, J. DeVore, WDF, Columbia River Laboratory, Battle Ground, WA, pers. comm.). Although these estimates are made primarily for run forecasting and are not meant to be statistically defensible, they provide an approximation of age changes during recent years. Prior to 1980, one or more age classes lacked CWT individuals, and the estimates made by WDF of age composition in the run were based on numerous assumptions that render the estimates totally unsuitable for use here (L. LaVoy, Fisheries Biologist, WDF, Wenatchee, WA, pers. comm.). No earlier age data that would be even somewhat representative of the Bright runs were found.

The time series of data on average size (weight) was not continuous and, when plotted, separated (with the exception of one data point) into three groups of points. Each group was associated with a unique period in time, geographic area in the river, type of fishery (gear) sampled, and data source (Fig. 8 and Appendix A). I used the Mann-Whitney U-test to make pair-wise comparisons of differences in location of the three groups with respect to average weight (Sokal and Rohlf 1981; STSC, Inc. 1987), and simple linear regression (Model I of Sokal and Rohlf 1981) to roughly describe the rate of change in average weight. The software package, STATGRAPHICS 2.6, was used for all statistical procedures.

Mean ages were plotted for return years 1980-86 and brood years (cohorts) 1974-80. No tests for statistical significance tests were conducted on the recent age data because of the short time series and extraneous influences, which are discussed below.

Results

These data indicate that Brights taken by in-river fisheries have declined in average weight (Fig. 8). The center group (codes c, d, and e in Fig. 8) was not significantly different than either the early group ($Z=-1.78$, $P=0.07$) or the late group ($Z=-1.45$, $P=0.15$),

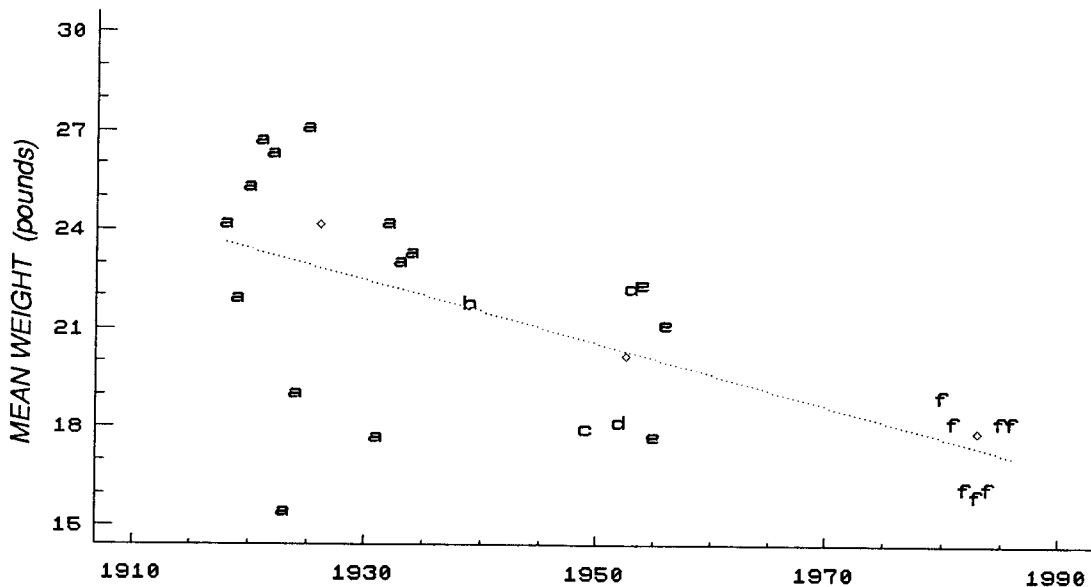


Figure 8. Trend in Bright mean weight, 1918-86. Data points form early (code a), middle (codes c, d, e), and late (code f) groups (code b not clearly part of any group), for which the weighted averages are shown (diamonds). The regression line (dotted; $W = 206.4 - 0.0953Y$, where W is the average weight (lb) and Y is the year) through all points shows approximate rate of change. Point values and sources are in Appendix A.

but the difference between the early and late groups was highly significant ($Z=-2.58$, $P=0.01$). The slope of the regression line suggested a rate of change (decline) in average weight of about $0.1 \text{ lb}\cdot\text{yr}^{-1}$ ($45 \text{ g}\cdot\text{yr}^{-1}$) for an overall loss of approximately 6.0 lb (2.7 kg) in average weight during the 68 yr between 1918 and 1986.

The mean age of Brights returning to the river declined rapidly (relative to rate of change in subsequent years) between 1980 and 1982, whence it remained relatively steady at approximately 3.1 yr through 1986 (Fig. 9). However, the mean age at return for broods (cohorts) shows an increasing trend over the 1974-80 brood year interval. The decline in the average age in the runs probably is a result of increased recruitment over a period of years (run size increased approximately five-fold between 1981 and 1986), which

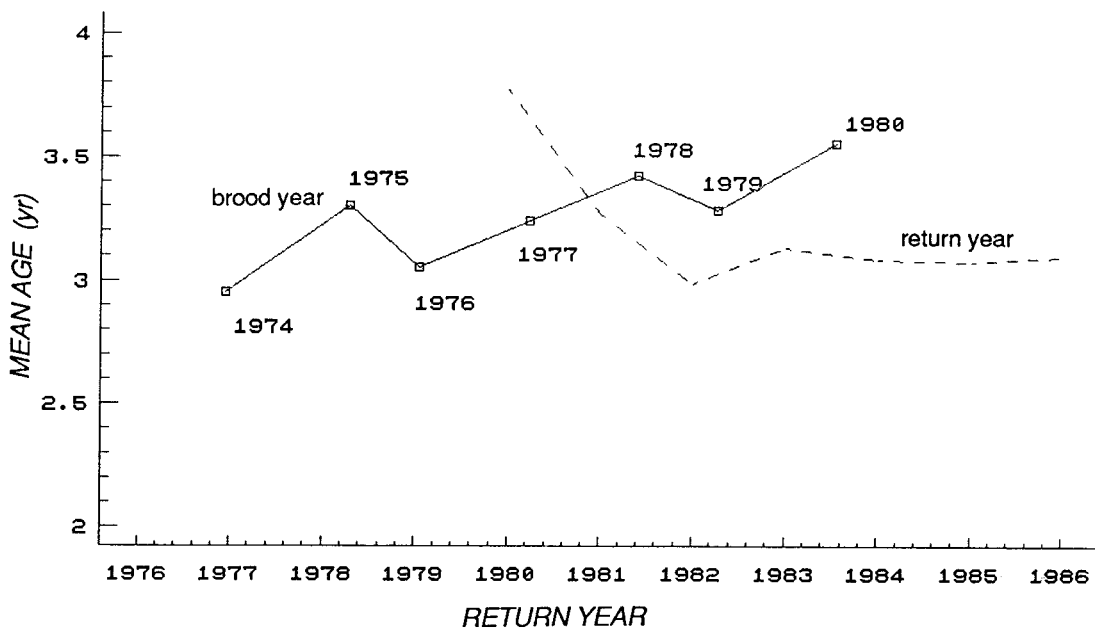


Figure 9. Mean ages of Brights by return year and brood year. Data points for brood years (shown beside points) are located, relative to the X axis, approximately when the 50th percentile of that brood returned to the river. Differing trends in standing crop (return year) and cohort (brood year) data are evident. Unpublished data from J. DeVore, Wash. Dep. Fish., Battle Ground, WA.

causes younger age classes to contribute larger proportions of the run. Thus, trends in mean age in return year data over short intervals may be more reflective of recruitment trends than of changes in the genetic or environmental factors directly influencing age at maturity of the stock. However, the preponderance of 2-yr-old jacks in recent years' runs may merit management attention (Fig. 10).

Discussion

The null hypothesis, that size and age of Brights in the spawning run was unchanged, could not be tested for age, but was tested and rejected for size (weight). This result is consistent with Ricker's (1980, 1981) hypothesis that declines in size and age of chinook salmon may be in part a result of changes within stocks,

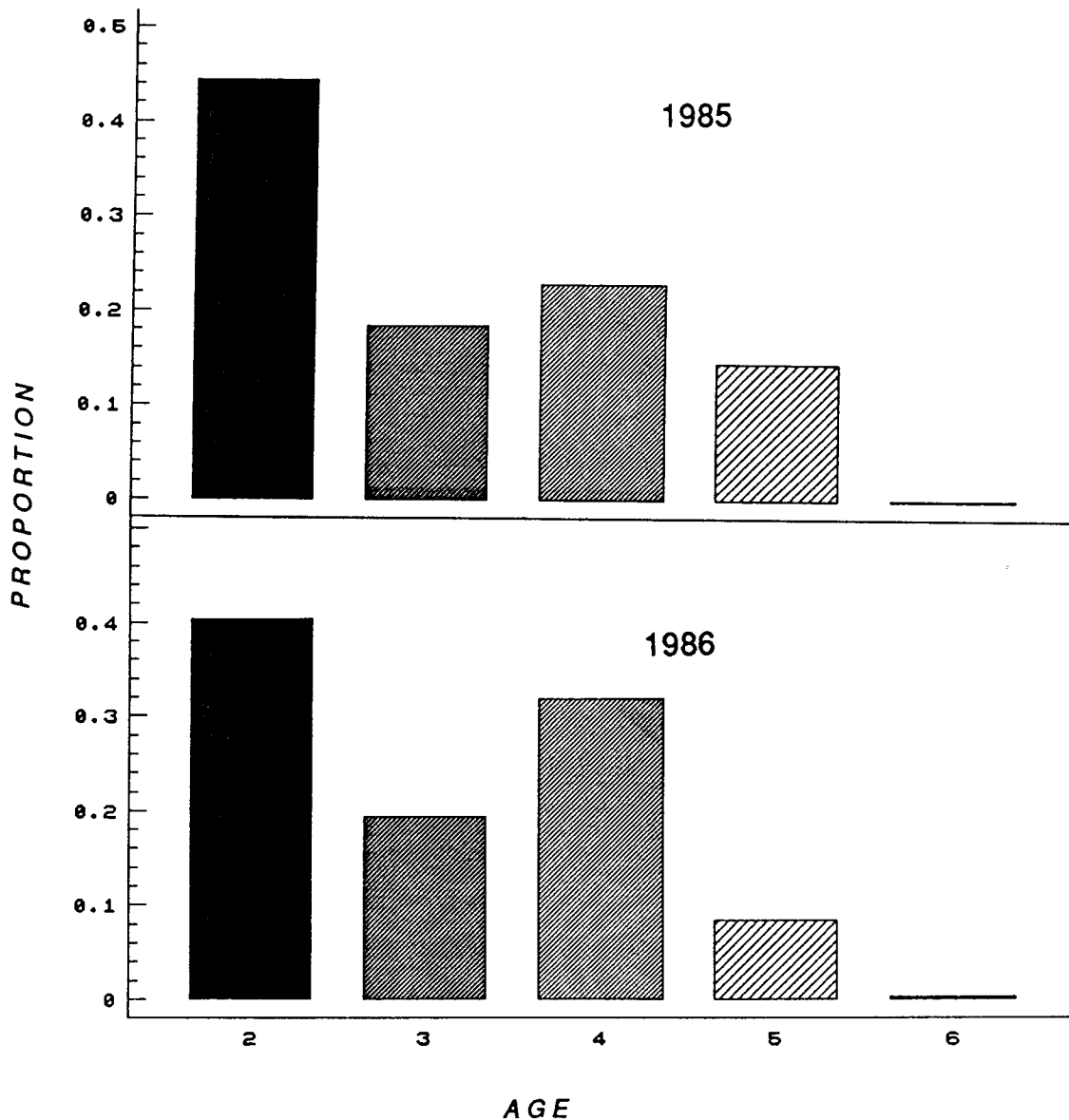


Figure 10. Estimated age composition of Brights returning to the mouth of the Columbia River in 1985 and 1986, years when run size was increasing (Fig. 5). A very high proportion of jacks (age 2) is common between the two years, which have similar age compositions overall. The high relative abundance of jacks in 1985 did not presage an increase in the relative abundance of age 3 fish in 1986. Unpublished data provided by J. DeVore, Wash. Dep. Fish, Battle Ground, WA.

rather than being a result solely of a relative loss of stocks producing the largest fish. However, the rate of decline estimated here is only about one-half and one-third of those estimated for the ocean fisheries in British Columbia and Southeast Alaska, respectively (Ricker 1980, 1981). Certain questions about the reliability of the data used in this analysis must be addressed to demonstrate that the noted decline probably reflects a real trend.

Size

A fundamental concern is the former identity or nature of the Bright stock and how well the data represent the stock. The distinctiveness of Brights was apparently first recognized by fisheries managers in the late 1940s when the Celilo Falls Indian dipnet fishery was closely examined. It became apparent then that the fall fishery took almost exclusively Brights, as opposed to tules originating in Bonneville Pool and the lower river. Some of the earliest samples used for this analysis may have been from portions of the late summer run, a likely precursor of Brights, or from the Bright stock as it was emerging to fill a fishery-created niche (discussed earlier). Size changes between the precursors and present-day Brights would still be of interest here.

The samples used for this analysis probably included unknown proportions of stocks other than Brights, particularly in samples from the lower river. However, between 1918 and 1934, lower river hatcheries (including those presently located on Bonneville Pool) were probably not yet contributing substantially to the tule runs (suggested in Wahle and Smith 1979). Also, it was not until the 1930s that Brights began to suffer habitat loss due to dam construction, so potential contribution of Brights to the fisheries prior to that time was probably unabridged. Brights, or their precursors, may have composed a major part of lower river catches of fall chinook salmon during fall seasons between 1918 and 1934. It is unlikely that the chinook salmon of other stocks that may be included

in the samples were sufficiently numerous and consistently large enough to cause a significant upward bias.

It is reasonable to assume that nearly all fall chinook salmon taken at Celilo Falls or above The Dalles Dam during most years since 1933 were Brights. The seines just downstream of Celilo caught some tules, but the dipnets at the falls rarely took them (Schoning et al. 1951; F. Cramer, pers. comm., 11/88), suggesting that Celilo Falls may have been the approximate upstream limit for the ripe tules. Inundation of Celilo Falls in March of 1957 (Cramer 1974) may be responsible for the large numbers of tules noted as far upstream as the Priest Rapids Spawning Channel from 1957 through the early 1960s (Meekin 1967a; Allen and Meekin 1973). No data from this period have been used in this analysis. The samples from Celilo Falls and the pools of The Dalles and John Day dams used for this analysis were probably almost exclusively Brights.

The sizes of fish in the samples are also a function of the size-selectivity of the capture gear, and the intensity and selectivity of downstream fisheries. The trap-caught fish measured by Chapman (1940) included 2-yr-old jacks and were probably more representative of the run than the significantly larger (by approximately 4.5 lb [2.0 kg], on average) than fish taken by gillnets at the same time (August) in the same lower river area. Water depth in trap areas may have had some influence on the size of fish available to the traps (e.g., larger fish may have avoided the traps by migrating in mid-channel) and removal of larger fish by gillnetters downstream of the traps may have reduced the average size of the trap-caught fish. In both cases the potential biases, most of which would reduce the average size in these early data, would probably make the present analysis and conclusion more conservative. The earliest size estimate from Celilo Falls (1939, point "b" in Fig. 8) further suggests that the lower river trap catches do not overestimate Bright size for the 1918-34 period.

The lower river gillnet fishery probably substantially reduced the average size of fish available to upstream fisheries (Rich 1940a, 1942; Gangmark 1957); hence, the Celilo Falls samples may be biased

downward. Dipnet catches at the falls, however, averaged 2.5 lb (1.1 kg) heavier than seine catches immediately downstream in mid-September, 1949 (Schoning et al. 1951). It is not known which gear is more representative, but dipnet catch data are far more available and are not likely to overestimate size in the run as a whole (considering that the lower river fishery removed larger fish). Bias in this intermediate group of data points (from Celilo) would not distort the apparent amount of total size decrease during the 1918-86 interval. Change over the entire period is reflected primarily in the difference between the early and late estimates of average size.

The gillnet catches in The Dalles and John Day pools, 1980-86, may be slightly biased upward. The size-selectivity of gillnets in this fishery during these years is discussed in a later chapter. Again, the effect of this potential bias is to make the analysis and conclusion more conservative.

The variability of size estimates is surprisingly large in the earliest group of points (the "a"s of Fig. 8). Changes in average size between years is often opposite for the trap-caught and gillnet-caught fish (Chapman 1940, Table 3), suggesting that the average weights in one or both fisheries do not consistently reflect average weights in the run. The low point of the cluster (15.5 lb [7.0 kg] in 1923) corresponds with a relatively very small sample (232 fish, only about 5% of the average number sampled in all 12 yr of the group), but its inclusion merely makes the analysis more conservative. There is no apparent explanation for the high variability in the earliest group of points.

Only the Celilo Falls dipnet catch (points "c," "d," and "e," in Fig. 8) was sampled by trained technicians, otherwise the data were recorded by fish buyers. There would be little incentive for the cannery to falsify their own records (source of points "a"), and there is no reason to believe that measurement errors by the buyers would be biased. WDF considers the pounds and numbers of fish reported on fish tickets during recent years to be reasonably accurate (D. Ward, Research Analyst, WDF, Olympia, WA, pers. comm.

1/89). The data used here are probably an unbiased, although not necessarily accurate, representation of the catch.

The 68-yr span represented by the size data (approximately 17 generations for Brights) is probably sufficient to avoid the effects of strong recruitment trends and cyclic dominance. Such effects are believed responsible for the opposing trends of brood year (cohort) and return year (standing crop) mean ages for recent years.

Age

The lack of reliable historical age data precluded an examination of long-term trends in Bright mean age. Approximations of recent age compositions in the run showed opposite trends when return year (standing crop) and brood year (cohort) data were compared, illustrating a potential danger in drawing conclusions from short series of standing crop data. Van Hying (1973) found greater variability in age of Columbia River fall chinook salmon using standing crop analysis as opposed to cohort analysis. Although size and age at maturity may change independently through evolutionary time, the two are closely related. Over the course of a few generations a decrease in mean age may have been associated with the observed decrease in mean size.

Conclusion

A decrease in average weight of Brights has probably occurred since the 1910s. Although Brights as we now know them may be a relatively recent development, the data used in the analysis are probably representative of the stock or its precursors. The data are probably biased, but the biases so far identified would tend to make the conclusion more conservative.

Some consequences of declining size and age were noted in the introduction and will be described further in a later chapter. The next chapter describes possible causes of the decline.

CAUSES OF SIZE AND AGE CHANGES

Introduction

The study's second objective was to gain a better understanding of factors that cause changes in size and age at maturity of Brights. Ricker (1980) ventured beyond a mere description of size and age trends of chinook salmon and proposed eight possible causes for the declines. His orientation was on mixed stock fisheries, and he emphasized the role that those fisheries could have in causing changes in size and age in the stocks, changes that probably have a genetic basis. The orientation of the present study, however, was on a single stock, and knowledge of the history and life cycle of the Bright stock facilitates a more detailed examination of factors that may have contributed to declines in its mean size and age at maturity.

A conceptual tool, which I call The Causal Sphere, is useful for understanding the network of factors that may influence size and age. Another tool, a mathematical model, is useful because it permits explicit treatment of individual factors, their interactions, and the magnitude of their influences on size and age. However, this model demands data that are usually not available or realistically obtainable. These two models are the first of several preliminary concepts and topics in this introduction that will lay the groundwork for considering the potential causes themselves.

The Causal Sphere

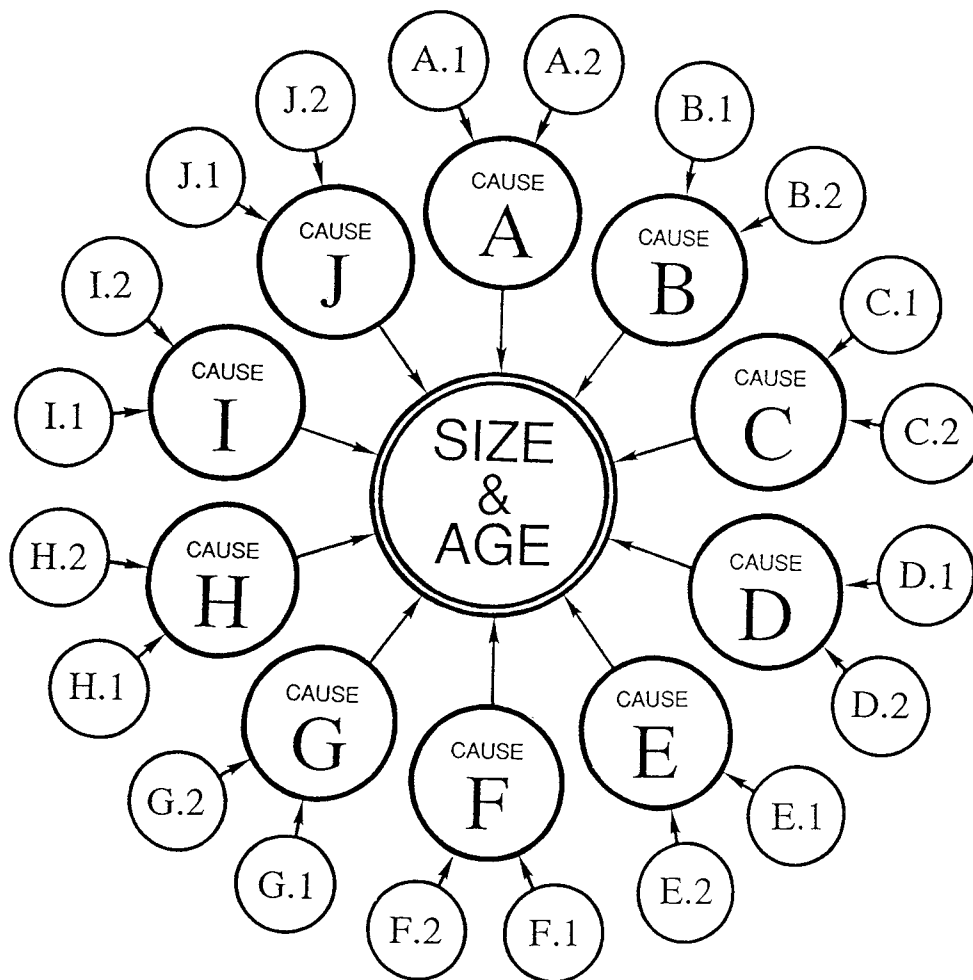
Earlier in this paper I used a conceptual model of simplified developmental environments and windows of opportunity to illustrate selection of life history types (Fig. 1). The sequence of developmental environments during the Bright life cycle is a natural organizational framework for examining potential causes for life history changes. Each environment, itself a collection of selective factors, may be thought of as an influence or contributing cause of

the observed size and age of spawners (Fig. 11). In addition to the environments, other factors such as the genome and recruitment trends are probably influential causes. These primary causes form a shell around the observed performance. Each environment or other cause is directly affected by a host of other factors (which may be viewed as secondary causes of size and age performances), each of which itself is a result of still other factors (tertiary causes), and so forth *ad infinitum*. For example, the Bright juvenile environment, a potential primary cause of adult size and age, could be affected by operation of the hydroelectric system (secondary cause), which is influenced by (among many other things) markets for electrical power (tertiary cause), etc. The result is a multilayered sphere of potential causes surrounding the observed stock performance.

The causes are neither discrete nor independent, but are an interwoven network. For example, environmental causes can, through selection, cause changes in not only the spawning run of the immediate generation (a phenotypic response), but also in the genome affecting size and age in subsequent generations (a genetic response). Large-scale climatic changes have the potential to affect all causes directly or indirectly, perhaps triggering a chain of cumulative or counteracting effects on size and age.

The Causal Sphere model draws heavily on the contextualistic world view (Pepper 1970), which considers empirical events as unique, ever-changing expressions of their settings (contexts). An event's context is a dynamic, never-ending fabric of processes and other events that cannot be unravelled. Strands of the fabric -- specific processes, relationships, and events -- can, however, be raised in relief and explored to a limited degree. Insight into how human actions and other environmental factors influence life history traits might be obtained thereby.

An alternative, more mechanistic (Pepper 1970) world view might couch the same problem of identifying causes of life history phenomena as a mathematical model whose terms must be experimentally defined. Such a model for predicting or explaining size or age at



- | | | | |
|----------|----------------------|----------|----------------------------|
| A | Juvenile Environment | F | Natural Migration Barriers |
| B | Migratory Pathway | G | Spawning Environment |
| C | Ocean Environment | H | Stock Genome |
| D | Ocean Fisheries | I | Recruitment Trends |
| E | In-River Fisheries | J | Unknown ? |

Figure 11. The Causal Sphere in two dimensions. Population traits, such as size and age at maturity in Brights, are influenced by a host of environmental and genetic factors (e.g., causes A-J). These causes are themselves the result of other factors (e.g., A.1, A.2), and so on. Hence, any observed phenomenon may be conceived as being surrounded by a sphere of innumerable direct and indirect causes, and the influence of any one or more causes may not be identifiable or measurable. Interactions between causes are not shown, but probably form a complex web.

maturity (Y) could take the form:

$$Y = a_1X_1 + a_2X_2 + \dots + a_nX_n + a_{x_1x_2}X_1X_2 + \dots$$

The model need not be linear, interaction terms may be very complex, and variable values would not always be untransformed. In short, the model could be very complicated.

Although providing a very explicit approach to a problem, such a quantitative model demands far more information about natural systems than is usually available. It is often a tremendous accomplishment to identify the major variables and their qualitative influence (+ or -) on the response variable. Rarely, if ever, can we define the forms of the terms, the magnitude of their coefficients, and particularly the interaction terms.

My approach to identifying the causes of changes in size at maturity of Brights follows more the contextualistic perspective. I explored the life cycle of Brights, pausing to raise in relief the factors that seem most influential on size at maturity. Understanding these factors and potential interactions requires a groundwork in genetics and other relevant concepts.

Genetics

Heritability of Size and Age at Maturity In order for the genome to be a potential factor in size and age declines, the traits must have some genetic basis, i.e., they must be heritable (defined in Appendix B). Numerous studies provide evidence for heritability in salmonids of age at first maturity (Konovalov and Ostrovsky 1980; Gjedrem 1983, 1985; Iwamoto et al. 1984; Glebe and Saunders 1986; Ritter et al. 1986) and size at maturity (Gjedrem 1983; Gjerde 1986). Selecting for both large size and early maturity in chinook salmon, Donaldson and Menasveta (1961) apparently (see Gjedrem 1983) caused an increase in growth rate and decrease in age at maturity in one generation. Hershberger (1976b) found that the proportion of chinook salmon returning as 2-yr-old males ("jacks") was an inverse function of both paternal and maternal ages. Ricker (1980) estimated a

heritability (h^2) of about 0.30 for chinook salmon age at maturity from Donaldson's work (presented in Ricker 1972, Table XII). Heritability of age at maturity in Chinook salmon was estimated at 0.37-0.48 based on a one-generation study at Oregon Department of Fish and Wildlife's (ODFW) Elk River Hatchery (T. Downey, ODFW, Springfield, OR, pers. comm., 4/88). Heritability for age at maturity has been estimated at 0.39-0.49 for Atlantic salmon (*Salmo salar*) and 0.21-0.26 for rainbow trout (*O. mykiss*; Gjedrem 1985).

Such relatively high estimates of heritability, considering that size and age are closely associated with "fitness" components (e.g., fecundity; see CONSEQUENCES OF CHANGES IN SIZE AND AGE, p. 155), are inconsistent with the expectations of genetic and life history theory (Falconer 1981; Riddell 1986). Heritabilities are difficult to measure precisely (Falconer 1981) and may be easily biased toward overestimation (Gjerde 1986); hence, the estimates above may be exaggerated. However, complex interactions among selective factors, high correlations between traits, and/or spatial-temporal environmental variability may also favor retention of genetic additivity for size and age. Regardless of theoretical considerations, the heritability of size and age at maturity of chinook salmon appears, on the surface, to be well established. However, measuring heritability of these traits may not be as straightforward as some investigators may believe.

Numerous known and potential correlations between traits confound interpretation of breeding study results. Age at maturity, size at maturity, growth rate, egg size, fecundity, spawning behavior, egg and fry survival, fry size, and fry growth rate have all been shown, directly or indirectly, to be interrelated (Fig. 12). Even ocean distribution is known to be genetically influenced (Nicholas and Hankin 1988) and could conceivably differ within stocks based on genetic characters that are correlated with one or more of the traits listed above. Most of these traits are easily measured; however, other traits that are unknown or immeasurable could also be related and influential. Because of these complex correlations, we cannot be certain which genetic traits were inherited by the

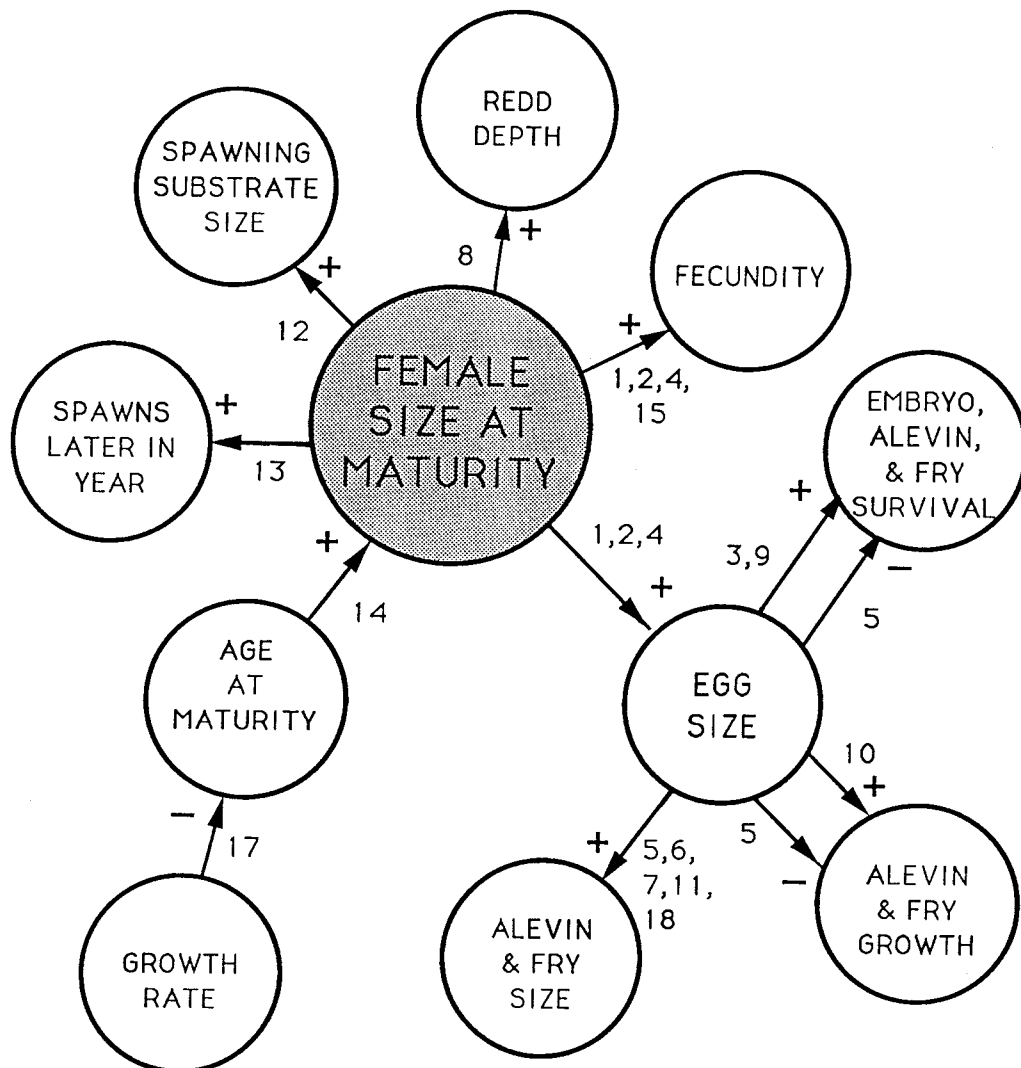


Figure 12. Some traits directly or indirectly correlated with female size at maturity. Pluses and minuses represent the nature of the correlations; numbers are reference sources:

- | | |
|---------------------------------|--|
| 1 Rich 1925 | 10 Gjerde 1986 (review) |
| 2 Rounsefell 1957 | 11 Smoker 1986 |
| 3 Bagenal 1969 | 12 Chapman 1988 (hypothesized) |
| 4 Mathews and Meekin 1971 | 13 This study (Fig. 14) |
| 5 Fowler 1972 | 14 This study (Fig. 13) |
| 6 Iwamoto et al. 1984 | 15 Hankin and McKelvey 1985 |
| 7 Thorpe et al. 1984 | 16 Weatherley and Gill 1987 |
| 8 van den Berghe and Gross 1984 | 17 see citations in "Growth and Age at Maturity" (p. 59) |
| 9 Hardy 1985 | 18 Thorpe et al. 1984 |

progeny and selected by their environments when parents of certain phenotypic ages or sizes were bred (see Lande 1982). Therefore, we must be fully cognizant that the heritable basis for size and age may rest on, or be interwoven with, a multitude of other genetic traits.

An intriguing and very relevant finding from some of these breeding studies is that inheritance of age at maturity is probably sex-related. Crosses of 2- and 3-yr-old male chinook salmon with 3-yr-old females showed that paternal age apparently influences the age at return of only the male progeny (Ellis and Noble 1960). Ricker (1980) noted that Donaldson's data (Ricker 1972, Table XII) showed that age at maturity was "sex-limited," because progeny matured at ages similar to that of the parent of the same sex. At Elk River Hatchery (ODFW), male chinook salmon that were progeny of jacks matured earlier than adult-sired males, but there was no difference in age at maturity between the female progeny of the two sire age classes (Nicholas and Hankin 1988). Likewise, no direct relationship was found between occurrence of jacks and average female age in chinook salmon populations of Oregon coastal streams (Nicholas and Hankin 1988). In a study of sockeye salmon (*O. nerka*) in a Soviet lake, inheritance of freshwater and marine ages was determined to be "linked with the sex" (Konovalov and Ostrovsky 1980, p. 326). In coho salmon (*O. kisutch*) sex-related effects were found in progeny length, and maternal and paternal influences were found in growth rate and possibly development rate, respectively (Iwamoto et al. 1984).

Sex-related inheritance is less remarkable in light of the more fundamental and major differences between the salmonid sexes in occurrence of meiotic multivalents, tetrasomic inheritance, and recombination frequencies (Allendorf and Thorgaard 1984). Because of sexual dimorphism in size and age at maturity of chinook salmon, selection on those traits could operate differently on the two sexes. (Evidence is presented in a later chapter to show that in-river gillnet fisheries for Brights may be doing precisely that.) Sex-related inheritance for the traits could enable divergence between

the sexes without changing the average trait values for the population as a whole.

Selection for Quantitative Traits Size and age at maturity are quantitative (or metric) traits that show continuous variation resulting from simultaneous segregation of many genes (Falconer 1981). Age at maturity, which falls into discrete classes, is considered a quantitative trait, because which class (age at maturity) a particular animal occupies is determined by the action of many genes operating over a continuous range. The effects of the individual genes are too small to be measured, but methods are available to describe the heritability and selection of the traits themselves (Appendix B). These descriptive measures are most useful under controlled mating conditions and are of limited applicability to natural populations, whose environments and mating strategies may be unknown or uncontrollable. In this study, the measures provide approximations of the hypothetical effects of some size- and age-selective factors for which data are available.

I must clarify selection for and selection against values of a trait. Selection is the process whereby the parents of the next generation are chosen, and conventional breeding experiments often choose for extreme trait values (e.g., large size, early maturity) in the parents. This study focuses on many factors that remove individuals from the potential breeding population based on extreme trait values; that is, they select against an extreme by causing differential mortality or reduced fitness among individuals possessing that extreme. These factors actually select for the opposite extreme. For example, a fishery taking the largest individuals selects (in a genetic sense) for small size because it causes smaller fish to be proportionately better represented in the population of potential spawners. Because a decline in size has been noted, we are particularly interested in identifying factors that select for small size and/or early maturity by killing or otherwise

reducing the fitness of Brights that would be larger or older at maturity.

Relationship Between Size and Age at Maturity

Size and age at maturity are directly related (Fig. 13), but only one of the two traits may be the basis for selection by a given factor or may be important for particular concerns. For example, size is the selected trait in fisheries with minimum size limits (e.g., commercial troll; given that some nonretained sublegal-sized fish survive to spawn), size-selective gears (e.g., gillnets), and/or methods of operation that impose differential selection based on size (e.g., effort concentrated in rearing areas with high incidence of small fish). Adult size may also be selected by conditions during upstream migration, spawning, and egg incubation, among others. Because size is so closely related to fitness components, maintenance of certain size classes may be essential for stock productivity.

Age is the trait selected by at least two factors, natural mortality and fisheries in rearing areas. In both cases the longer the fish waits to mature, the more mortality to which it is subjected. These factors select for younger age at maturity.

Both size and age are considered in this study because they are so closely related. When evaluating potentially selective factors, however, one or the other trait will usually be examined. Generally, size will be considered the more important, because the trend observed was in average size. This trend could reflect a similar trend in average age, however.

General Methodology

Starting with the embryo in the incubation and early rearing environment, the succession of developmental environments encountered during the Bright life-cycle were examined for factors that could be responsible for declining size at maturity. The literature was

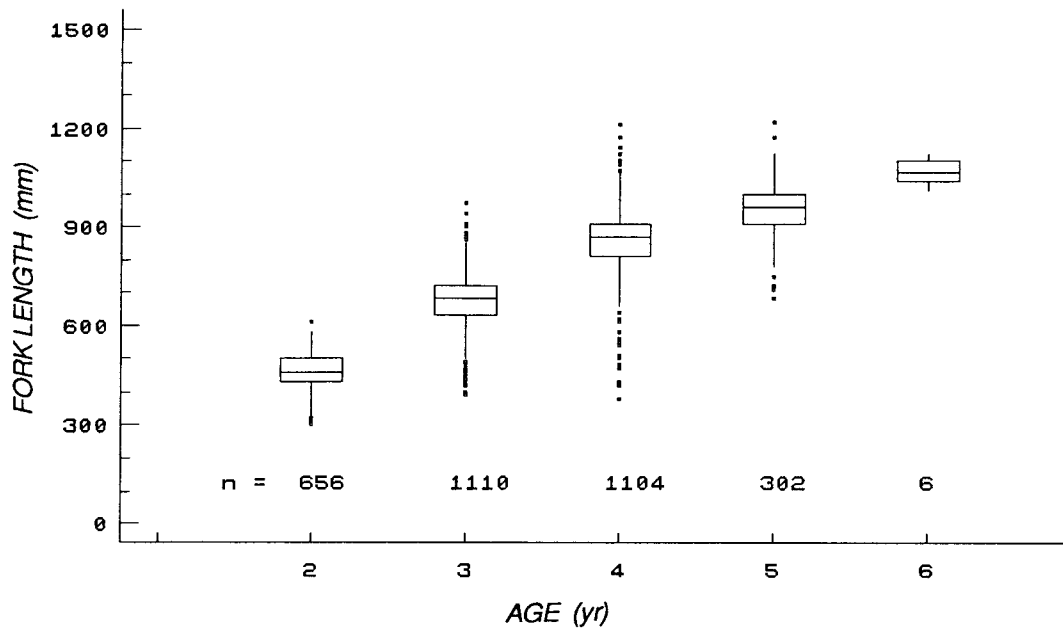


Figure 13. Box-and-whisker plot of length at age of Bright spawners, both sexes combined. Whiskers extend only to points within 1.5 times the interquartile range (STSC, Inc., 1987). Lengths of coded wire tagged Brights sampled in the escapements to Priest Rapids Hatchery and natural spawning areas in 1978-87 are combined. (Data from S. Markey, WDF, Olympia, WA.)

reviewed and data, when available, were collected for a more substantive analysis. Specific hypotheses, methods, results, discussion and conclusions are presented in the sections for each developmental environment:

- 1) Early Rearing
- 2) Outmigration
- 3) Ocean
- 4) Spawning Migration
- 5) Spawning

A concluding discussion melds findings from the five sections into a summary of potential causes of the declines.

Early Rearing

Factors at work during even the earliest period of life can influence the age at which individual Brights mature and the mean size and age in the stock. This association has not been widely acknowledged, so it is not surprising that relatively little effort has been applied to defining it. Defining this association is the purpose of this section, which emphasizes "maternal influences" and environmental factors affecting growth and selecting for traits that are correlated with adult size and age.

Maternal Influences

Early in life -- as embryos, alevins, and fry -- the young fish are still greatly under maternal influence; the progeny phenotype (e.g., egg and alevin size) is determined in large part by the dam's phenotype (e.g., body size; Fig. 12). "Maternal influences" are not the same as "maternal effects", a term used to describe mother-offspring similarities that are not based directly on genetic traits (Falconer 1981). Instead, maternal influences are important here insofar as they affect the viability of the progeny (due to size-related spawning success or egg size, for example), but not necessarily their phenotype for a particular maternal trait (e.g., size at maturity).

For example, if a large female is able to spawn in a more favorable location or if her larger eggs are more likely to survive, then her progeny should be relatively more abundant in some later developmental stages than those of a small female spawner. To the extent that size and age at maturity are inherited from the mother, the more viable progeny of the large spawner should also be somewhat larger, contributing to an overall greater mean size at maturity in their generation. However, the fact that the progeny inherited genes for large size is separate from the fact that their mother's size may have enhanced their probability of survival. In this case, maternal size (phenotype) influences the relative abundance of her offspring,

and, if her size at maturity is directly or indirectly heritable (genotype), may also have a bearing on their size at maturity.

Three maternal influences -- spawning time, spawning site, and egg size -- were examined. If these influences are correlated with spawner size or age, and if they are related to fitness differences in the offspring, then they may influence size and/or age at maturity of Brights. Size, rather than age, is the principal trait of interest. The null hypotheses are that the influences are unrelated to spawner size and to fitness differences in the offspring.

Spawning Time Cushing (1975, 1981, 1982) argues for the importance of a spatial-temporal match between reproduction of marine fishes and the production of food for the larvae. Similar "time-windows" models have been used to describe evolution of life histories in Pacific salmon (Thompson 1959; Becker 1970; Miller and Brannon 1982), which are reflected in Mullan (1987) and the environmental "windows of opportunity" model of this paper. Spawning time may be critical not just to match windows in the spawning environment, but to match the subsequent developmental stages of the offspring with time windows in their environments.

Data from known Bright female spawners at Priest Rapids Hatchery during 1979-87 (see Appendix C for CWT codes used) were examined for a relationship between spawning time (week of year) and female size (fork length [FL]). Data were obtained from the WDF CWT recovery database in Olympia, WA. (S. Markey). Recoveries of CWTs in weeks prior to 42 (mid-October), assumed to be unspawned fish that were disposed of as surplus (G. Osborne, WDF, Manager, Rocky Reach Hatchery, pers. comm.), were not used in the analysis. Recoveries during later weeks were assumed to fairly approximate the time that spawning would have occurred in nature. No data were found to test for a relationship between time of spawning and progeny fitness.

On average, females spawning earlier in the season were larger than those spawning later for the years examined (Fig. 14). The

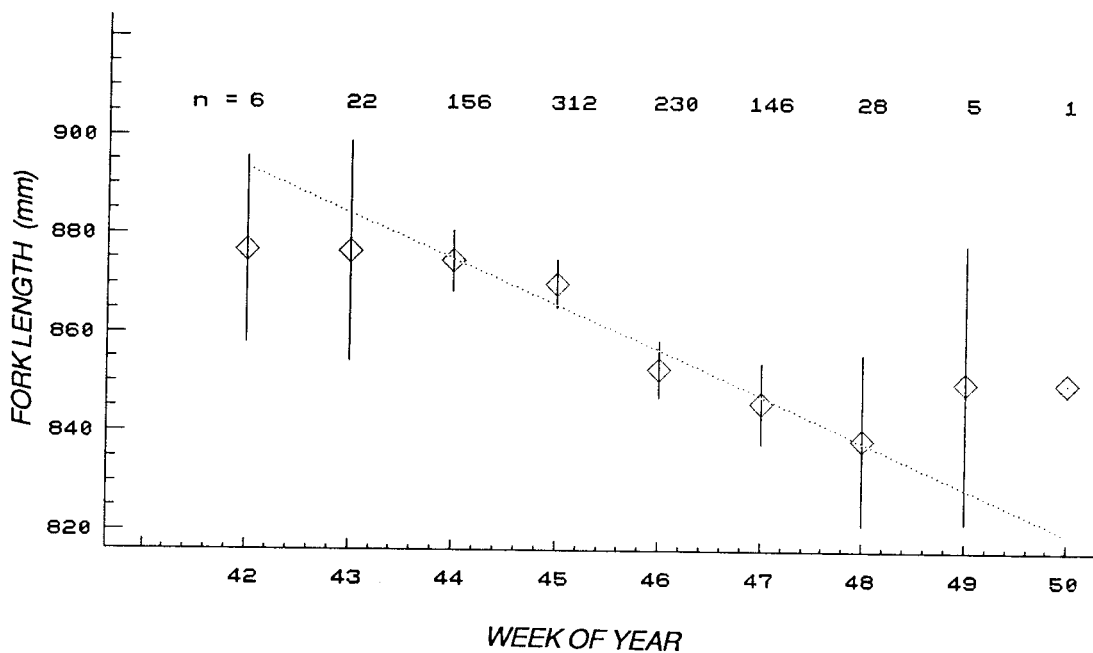


Figure 14. Trend in size of Bright females by week of spawning. Week of tag recovery at Priest Rapids Hatchery in 1979-87, combined, of Brights coded wire tagged as juveniles at the hatchery, is assumed to represent actual time of ripening and spawning. Mean length and SE are shown for each week. Recoveries prior to week 42 were omitted because they are believed to be from fish disposed of as surplus; hence, the date of tag recovery would not reflect time of spawning. Trend line is from simple regression: $1281.2 - 9.231W$, where W is week of year when spawned, $n = 906$, $t = -3.85$, $P < 0.001$, and $r^2 = 0.02$. (Data from S. Markey, WDF, Olympia, WA.)

slope of the linear regression of female length on week is negative and highly significant ($P < 0.001$). Female mean length for all years combined declined by 9.2 mm per week, or a total of approximately 74 mm for the 8-wk range spanned by the data. Eliminating the few data points for weeks 42, 49, and 50 increased the rate of decline in the slope and its statistical significance. This decline in size during the spawning season has been noticed, but not measured, by personnel at Priest Rapids Hatchery (G. Osborne, WDF, Manager, Rocky Reach Hatchery, pers. comm.). Extremely weak and nonsignificant correlations among year, annual average size, and annual average week

of spawning indicate that this trend toward smaller spawners in later weeks is not strictly a result of trends across years.

Whether time of spawning within the season confers any fitness advantages on the progeny of early-spawning large females or late-spawning small females is not yet known. Differential development times for eggs of large and small females (e.g., Smoker 1986) may make the different spawning times adaptive for placing the fry within the time windows of opportunity for their environments. If the thermal shift caused by completion of Grand Coulee Dam in 1941 (Jaske and Goebel 1967) necessitated a shift to a later time of spawning, then older (larger) fish with longer generation times may be slower in adapting. There is evidence (see *In-river Fisheries*, p. 110) that Bright run timing is becoming later, particularly for smaller fish. If those later-spawning females were also smaller, then small size would have been relatively more fit since 1941 (assuming that early season water temperatures have been adversely high since then), and the increased fitness of small females could have contributed to the observed long-term decline in size and age. Other reasons may also account for or contribute to this trend, such as artifacts of hatchery rearing or broodstock holding, smaller females taking longer to reach the spawning grounds, etc.

Spawning Site Fewer embryos or alevins will survive if, due to her size, the maternal spawner is unable to obtain or effectively use a favorable spawning site. Sites are definable in terms of depth of the water, flow velocity, substrate characteristics, and depth within the substrate. There are few data and little information available to relate spawner size to site characteristics and site characteristics to progeny viability. Therefore, this discussion will be largely hypothetical.

If dominance were a function of size, and if certain sites were favorable for females of many sizes, then smaller females could be forced to spawn in poorer habitat. Winter low flows and temperatures in the mid-Columbia where Brights spawn may have favored spawning in deep water rather than along the shallow stream margins where redd

dewatering and freezing could inflict high embryo and alevin mortality (Chapman et al. 1986). On Vernita Bar, a heavily used Bright spawning area just below Priest Rapids Dam, spawning begins in deeper locations and progresses into shallower areas, suggesting that the shallower areas are perceived to be less favorable (Chapman et al. 1986). Alternatively, the deep-to-shallow spawning progression could reflect the progression of increasingly smaller spawners occupying habitat to which they are better suited. Poor visibility has prevented divers from observing potential differences in size between deepwater and shallow-water spawners (G. Swan, National Marine Fisheries Service, Pasco, WA, pers. comm.; D. Chapman, Don Chapman Consultants inc., Boise, ID, pers. comm., 1/89).

Only in recent years have redds in shallow areas of Vernita Bar received some protection from adverse flows. Regulation of the Columbia River has moderated the cold temperatures (Jaske and Goebel 1967) and low flows of winter, but has greatly increased weekly and daily flow fluctuations (up to 4.5 m in 24 h; Chapman et al. 1986) due to variable demand for hydroelectricity (Fig. 15). Massive egg and fry mortalities have been attributed to extreme short-term flow reductions (Bauersfeld 1978). Flow restrictions have been imposed at Priest Rapids Dam to discourage spawning at high elevations on Vernita Bar and to protect redds from dewatering (FERC 1988). These restrictions should improve the survival chances of eggs and alevins in shallow-water redds, regardless of maternal size.

Not only are the relative sizes of deepwater and shallow-water Bright spawners unknown, but it is also not known how primitive conditions and recent decades of regulated variable flows may have selected against the progeny of shallow-water spawners. I can only say that, despite the variability, regulated flows in recent decades may have selected less harshly against the margin spawners, which may have been the less dominant and later-spawning smaller fish. Hence, the fitness costs of being a small female spawner may have declined with changes in the spawning environment, hence contributing to the

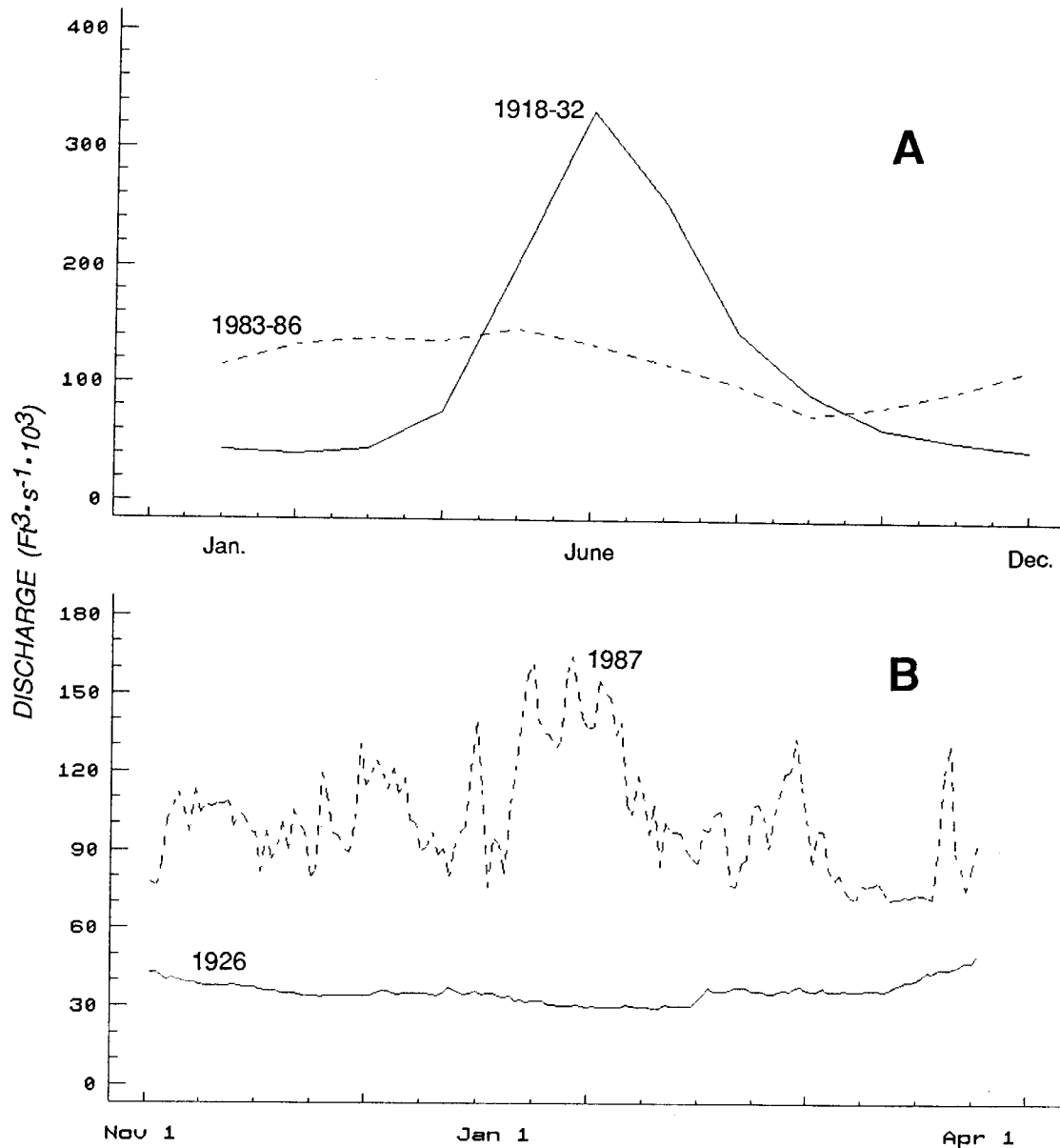


Figure 15. Historical and recent flow patterns in the Hanford Reach immediately below Priest Rapids Dam. (A) Monthly average flows for the early period (averaged for calendar years 1918-32, except 1925-26; solid line) show a distinct peak in June with minimum flows in winter. Presently (1983-86; dashed line), storage reservoirs allow a leveling and reshaping of the hydrograph with higher flows during winter when local demand for hydroelectricity is greater. (B) Similar short-term flow shaping to meet power demand has caused dramatic day-to-day and even hour-to-hour variations in river level during intragravel development of Bright embryos and fry (e.g., in 1987), compared to the relatively constant short-term flows of predevelopment years (e.g., in 1926). (Data from USGS, Portland, OR and Pasco, WA for gage station 12472800.)

long-term decline in size. There is little evidence to prove or disprove such an hypothesis, however.

There is also little evidence relating size of female chinook salmon with size of spawning substrate chosen or depth of egg burial. Sockeye salmon have been noted to spawn in much smaller substrates than chinook salmon (Chambers 1956). If this is a function of fish size, then we might expect selection of larger or smaller spawning substrates according to size of female Brights. Chapman (1988) states generally that there is a positive correlation between fish size and spawning substrate size. The depth to which the egg pocket is buried in the substrate has been positively correlated with female size in coho salmon (van den Berghe and Gross 1984).

There is some evidence relating egg and alevin viability to redd site characteristics. Although greater depth presumably protects against redd disruption during winter freshets (van den Berghe and Gross 1984), such would not necessarily be advantageous for Brights, which are subjected to winter drought and little streambed movement (Chapman et al. 1986). However, O'Malley (1920) suggested that deeper egg burial reduces the amount of light available for growth of fungus that could threaten the embryos. Large substrate size, which permits greater intragravel flow and alevin movement, has been associated with increased survival to emergence in chum salmon (*O. keta*) (Dill and Northcote 1970) and with survival, size, and development rate of pink salmon (*O. gorbuscha*) embryos and alevins (McNeil and Ahnell 1964; Wells and McNeil 1970). However, large substrates may allow more eggs to be lost to turbulence and predation (McLarney 1967, cited in McNeil 1969). Substrate size itself is a function of stream gradient, water velocity, and sediment load, all of which may contribute to apparent relationships between gravel size and measures of fitness of embryos and alevins (McNeil 1969; Chortley et al. 1984).

The site a female Bright chooses to deposit her eggs greatly influences the fitness of her progeny, but there is much to be learned about how female size relates to redd site and how site characteristics influence embryo and alevin viability. It is

possible that formerly low apparent spawner densities (Watson 1970; Rogers and Hilborn 1988) and flow and temperature changes since 1941 modified the competitive and physical environments for spawning, perhaps increasing the relative fitness of small spawners (see Spawning, p. 140).

Egg Size Egg size is probably the best understood of the three maternal influences considered here. Egg size is known to be related to female size in salmonids, with larger females producing larger eggs (Rich 1925; Rounsefell 1957; Mathews and Meekin 1971).

The relationship between egg size and embryo/alevin/fry fitness has also been studied, but with results that conflict and that may not apply to natural production. One study found that Columbia River tule fall chinook salmon from large eggs had higher mortality, initially larger size, and slower growth rates as eggs, fry, and fingerlings than did those from small eggs (Fowler 1972). Rainbow trout fry from large eggs had higher survival to swim-up than fry from small eggs in other work, however (Hardy 1985). Likewise brown trout (*S. trutta*) fry from large eggs (larger fry) had significantly greater survival than those from small eggs (smaller fry) under food deprivation (Bagenal 1969). Other salmonid egg size studies reviewed by Gjerde (1986) showed that large eggs produce young with greater early (up to four months of age) growth and perhaps better survival. Chum salmon fry from large-egg females were larger after one month of growth than those from small-egg females (Smoker 1986). Large Atlantic salmon eggs produce fry that are larger than fry from small eggs, but the size advantage persists less than a year (Thorpe et al. 1984). No survival advantages of embryo size were observed in this last study.

There is agreement that large eggs produce initially larger young that retain their size advantage for a few weeks or months. The duration of similar maternal "effects" on fry and fingerling size appeared directly related to egg size differences in a study on coho salmon (Iwamoto et al. 1984).

Agreement is lacking on the effects of egg size on survival, but some of the disagreement may be attributable to species, stock, and methodological differences among the studies. Probably without exception the studies were conducted under controlled hatchery conditions, so there must be some question whether relative survivals of small and large eggs, and the fry that issue from them, would be similar in the natural environments. Large eggs may require higher dissolved oxygen concentrations (McNeil 1965), and shorter development times (Smoker 1986). However, the times and sites at which the different-sized females spawn could compensate for the differing requirements of their larval young. The ability to fast during the first feeding stage (Bagenal 1969) would likely be an advantage for large fry in a natural environment, but such an advantage would not be evident in studies providing regular and liberal feedings. Fry size can be an advantage for avoiding predators (Taylor and McPhail 1985), although at least one study, perhaps because of an inadequate study design, found that it was not (Fresh and Schroder 1987). In nature, large fry may be better able to establish and hold territories than fry that are smaller but faster growing (Thorpe et al. 1984).

The correlation between female size and egg size is clear, but the relation between egg size and fitness in the young is not, particularly for natural incubation and rearing environments. Although potential advantages of egg size offer a tantalizing hypothetical solution to riddles about chinook salmon life histories (e.g., Hankin and McKelvey 1985), those advantages are far from being proved. I can only conclude that progeny may enjoy fitness advantages due to egg (and, therefore, maternal) size.

Maternal Influences Summary Maternal influences form a phenotypic bridge between parent and offspring generations. The bridge in this case is the role played by size of the female spawner in determining how many of her young survive to adulthood. Female size is associated with egg size, spawning time, and perhaps with spawning site chosen. Egg size is the only maternal influence, that

I am aware of, that has been investigated for potential fitness effects on the progeny. Large eggs produce initially larger fry, but beyond that little is known about whether egg size is adaptive for particular environments.

Changes in spawner density, temperature regime, flow variations, and other factors in the Bright spawning environment may have contributed to the observed decline in size by modifying the expression of maternal influences. For example, if small females were more likely to spawn in shallow margin areas and the penalty for doing so was lessened by a moderation of flow variability during incubation, more small fish could be expected in later generations as a consequence.

Growth and Age at Maturity

Growth rate is an essential element in determining the life histories of salmon and other diadromous fishes (Gross 1987). It is among the very few early life performances that has a demonstrated association with size and age at maturity. Unlike maternal influences, which do not directly affect size and age at maturity of individual fish, growth rate can affect both the age (and hence size) at which individuals mature, as well as their relative viability. This section will consider the influence of juvenile growth rate on age at maturity of individuals; the next section will discuss how growth helps determine which individuals contribute to the spawning population.

Although heredity is a known factor in determining growth rate (Alm 1959; Donaldson and Menasveta 1961; Ricker 1972; Naevdal 1983), it is the environmental factors that are of interest here. Might different growth conditions in the freshwater environment have contributed to the observed decline in mean size and age? Here I will present evidence that juvenile growth rate is associated with age at maturity; later I will discuss changes in the early rearing environment of Brights that could influence growth rate and contribute to the decline.

There is considerable evidence that growth rate during early life and age at maturity are closely associated. As might be expected, the effects of juvenile growth on age at maturity are most apparent in the youngest age classes of mature fish. In Atlantic salmon, precocious parr are among the fastest growing of their age class up until the onset of maturation (Glebe and Saunders 1986). A significant increase in the percentage of mature age 1+ Arctic char (*Salvelinus alpinus*) was associated with intensified feeding in all of the several life history types studied by Nordeng (1983). Male rainbow trout maturing at 1 yr of age were approximately 15% heavier than the average weight of siblings in one study (Gall 1985). Coho salmon released from hatcheries at large size return more jacks (2-yr-old males that mature in the same year as their release) relative to adults (mature after one ocean winter) (Lorz 1971; Johnson 1970; Bilton et al. 1982). Alm (1959) provides further examples of growth effects on age at maturity in his excellent review; Wallis (1968) and Lorz (1971) also provide good reviews for anadromous Pacific salmon and trout.

This inverse relationship between juvenile growth rate and age at maturity has also been noted in Columbia River chinook salmon. Average lengths of groups of mature fry (age 0+) found at various locations in the Columbia River Basin ranged from 16% to 23% larger than the average lengths of sympatric immature specimens (Rich 1922). Returns of extraordinary numbers of spring chinook salmon "minijacks" (same life history as a coho salmon jack) to WDF's Cowlitz Hatchery were attributed to releases of unusually large smolts (Paul Peterson, Manager, Cowlitz Hatchery, pers. comm.; see also Mullan 1987, p. 89).

Size is obviously a function of both growth rate and time. In the examples used here, size differences between groups within a study reflect differences in growth over an approximately equal time period.

There are apparent exceptions and some noteworthy considerations bearing on the general rule that early maturity is associated with rapid juvenile growth. Iwamoto et al. (1984) found an inverse, but nonsignificant, relationship between size and early

maturation (as jacks) among full-sib groups of coho salmon involved in a breeding study comparing jack and adult sires. This finding opposes those of the studies previously mentioned. Alm (1959) cites comparisons between populations of fish wherein the slower-growing population matured at an earlier age, but he rightly points out that genetic differences are probably the cause. Populations develop genetically based life histories in response to unique growth, mortality, and fertility patterns in the population and its environments (Stearns and Crandall 1984). The coho salmon exception noted above (Iwamoto et al. 1984) could be explained by differences in growth being too small to override genetic control of maturation within the jack- and adult-sired groups. Environmental influence on the age at maturity of individual fish is probably limited to modifying the expression of genetic potential.

Most of the studies above document increases in the relative abundance of the youngest age classes associated with rapid juvenile growth, but there is little evidence that the distribution of the older classes of mature anadromous salmonids is related to freshwater growth. The later a Bright is likely to mature based on its inheritance (Brights can probably mature at ages 1-7, although ages 2-6 are the most common), the less sensitive its age at maturity probably is to growth during early (freshwater) rearing. Thus, the genetic potential for later maturity buffers the effects of between-year variations in growth potential in the early rearing environment on size and numbers of fish in the runs of subsequent years. Growth during later life stages continues to be influential in determining age at maturity, but this topic will be reserved for later discussion.

The association between growth rate and age at maturity is almost certain, but whether improved growth causes early maturity is less so. Gjedrem (1985) and Gjerde (1986) caution that maturation may in fact cause increased growth (rather than *vice versa*), or that both growth and maturation may be stimulated by sex hormones. However, the former hypothesis is not consistent with other findings, and the latter is not necessarily relevant for the immediate problem. Onset

of maturation actually retards, at least momentarily, the growth rate of the faster growing, early maturing individuals (review in Alm 1959; Gall 1985; Thorpe 1986). Hence, the immediate process of gametogenesis (maturation) does not improve growth. Steroid hormones are indeed known to influence growth rate in fish (Lorz 1971; McBride and Fagerlund 1973; Weatherley and Gill 1987; but see Sower et al. 1983). However, of principal importance here is that environmental factors promoting growth (e.g., better feeding conditions, Nordeng 1983; warm winter temperatures, Dirin-Khalturin 1982) are also likely to promote earlier maturity; how the effects of the environmental factors are mediated is of lesser concern.

In an evolutionary sense, early maturity is adaptive for quickly colonizing and fully exploiting favorable habitats. Rapid growth can shorten the generation time (and increase survival, as will be seen in the next section), thereby favoring population growth until carrying capacity is reached (Larkin 1981). By the same association, an older age distribution might be expected when population densities are high and growth is relatively poor. For Brights and other Columbia River anadromous salmonids, a maturity schedule that is sensitive to growth conditions would be an asset for recolonizing habitats frequently disrupted by major geologic events (Li et al. 1987).

Hatcheries, which are increasingly used for production of Brights and other anadromous salmonids in the Columbia River, are rearing habitats where juvenile growth conditions are nearly always favorable. The implication of such favorable growth for Bright age at maturity may now be apparent, but a later section will investigate the relation in detail.

Unfortunately, the effects of changing growth conditions on age at maturity may not be distinguishable from the effects of other causes, particularly genetic changes due to selection. Fisheries (or other factors) may promote reduced age and size at maturity by reducing densities during life stages when growth is density dependent (Miller 1956; Riddell 1986; Thorpe 1986), or by selecting for early maturity and/or slower growth genotypes (Schaffer and Elson

1975; Ricker 1980, 1981), or both. A changing genome due to selective fisheries is certainly the more threatening scenario, because the process and its effects are largely irreversible (Ricker 1980). Therefore, as long as the effects of the two causes remain indistinguishable, prudence requires that the growth hypothesis not be simplistically embraced to the exclusion of the genetic hypothesis. Human activities could cause severe and relatively immutable changes in the life histories of important species if resource managers mistakenly believed that the changes were merely easily reversed phenotypic responses.

To summarize, growth conditions for juvenile Brights can influence age at maturity of individual fish, particularly those genetically predisposed to early maturity. Improved freshwater growth conditions in the natural and hatchery habitats may contribute to reduced size and age in the Bright run. How growth conditions can also affect the survival of individuals that might mature at different ages will now be considered.

Growth and Survival to Maturity

"The little fish that feeds well, grows well, swims quickly, evades predators and feeds better than ever" (Cushing 1975 p. 241).

That size confers survival advantages to fish, particularly in their early developmental stages, is virtually axiomatic (for example, Cushing 1975, 1981; Ricker 1976; Wooster 1983; Weatherley and Gill 1987). Might changes in freshwater growth conditions or size-selective mortality factors favor survival of faster- or slower-growing individuals? If so, could mean size and age at maturity be affected?

This section presents evidence supporting the association between size and survival, and discusses how environmental factors, by influencing growth rate, can also influence mean size and age in the spawning run. The emphasis is on how environmental factors determine which fish survive to mature, those that will be older or

younger, not on how the factors influence the age at maturity of individual fish.

Numerous studies have provided evidence that associate growth rate and survival to maturity. Hatchery time and size at release studies with Pacific salmon (e.g., review by Wallis 1968; Johnson 1970; Lorz 1971; Allen and Meekin 1973; Reisenbichler et al. 1981; Bilton et al. 1982) have firmly established the relationship between larger size at release and better survival to return. Maximizing size at release, within certain time constraints, is now a norm for some culturists (Seidel et al. undated). In the Columbia River, a greater portion of the smaller juvenile chinook salmon are apparently lost during the time it takes to migrate from the release point to the estuary (Dawley et al. 1986; Zaugg et al. 1986). Better survival has also been associated with larger smolt size within and among natural stocks of sockeye salmon (Ricker 1976; West and Larkin 1987). Scale growth comparisons in natural chinook salmon stocks confirm that juveniles with better growth and larger size at outmigration are more likely to survive to adulthood (Reimers 1973; Nicholas and Hankin 1988). Juvenile chum salmon with wider scale circulus spacing (i.e., the faster-growing individuals) apparently have had superior survival in nearshore rearing areas (Healey 1982). As the chum salmon grew, particularly through the 45-55 mm length range, size-selective mortality appeared to intensify, suggesting perhaps a change of predators concurrent with migration into more open pelagic habitat.

There is at least one exception to the wealth of evidence for an association between growth rate (expressed as size at a given time) and survival. Holtby and Healey (1986) found that smolt size (based on scale measurements) was "not consistently an important factor in marine survival," (p. 1956) for coho salmon from Carnation Creek (Vancouver Island, British Columbia, Canada) that smolted during 1971-82. Possible explanations for this contrary observation were not offered, nor are any immediately apparent.

Predation is the most commonly postulated cause of size-selective mortality. Aquaria tests with pink salmon and chum salmon

fry prey demonstrated that small size is a predation handicap that can be outgrown (Parker 1971). Size-related swimming speed may be the critical factor in avoiding predation (Taylor and McPhail 1985). Smaller juveniles may also be more vulnerable to parasites (West and Larkin 1987).

The available evidence supports the hypothesis that rapid growth is associated with higher survival. Growth is a self-reinforcing process, the greater the growth, the greater the opportunity to continue growing (Larkin et al. 1956; Cushing 1975, 1981). If size-selective mortalities consistently favor rapid growth, then they probably also favor early maturity. Hence, any factor that increases the selection against slow growth (e.g., intensified predation) could contribute to declines in size and age at maturity. However, because slow growth (and older age at maturity) can provide fitness advantages in other developmental stages (e.g., older, larger adults with superior spawning ability), genotypes for slow growth/late maturity and rapid growth/early maturity may exist in balance in a population (Gross 1987). Selection favoring rapid growth in some environments may be counteracted during other stages of development (Healey 1986).

The ability of growth to influence both age at maturity and survival to maturity is a cornerstone principle for considering the natural and artificial early rearing environments of Brights.

Hanford Reach Environment

Described as "remnant habitat" (Becker 1985), the 94-km Hanford Reach is the last free-flowing stretch of the Columbia River between Bonneville Dam and Canada (Fig. 3). This area, the primary source of natural Bright production (Norman 1984; Howell et al. 1985a), is not pristine, however. The U.S. Atomic Energy Commission Hanford Nuclear Reservation, which contains or borders most of the Hanford Reach, has both changed and preserved Bright rearing habitat since the early 1940s. Since Grand Coulee Dam was closed in 1941, the hydroelectric power system has altered Hanford Reach flows to meet its needs,

largely irrespective of impacts on Bright production. Becker (1985) provides a good description of the Hanford Reach environment.

This section examines the incubation and early rearing environment in the Hanford Reach to determine if changes in temperature, flows, and other environmental factors may have contributed to declines in size and age in the Bright runs. How some of these factors may contribute to changes in the relative fitness of small or large female spawners was described in the earlier section on maternal influences. How these factors relate to growth of juvenile Brights, which is closely associated with their size and age at maturity, was of interest for this part of the study.

The Hanford Reach gravels receive the fertilized Bright ova beginning in mid-late October (peak in early-mid-November) (Howell et al. 1985a) as the water temperature declines below 15°C (Fig. 16). This is similar to the generalization by Chambers (1956) that fall chinook salmon in the Columbia River Basin spawned when temperatures dropped below 13.3°C (56°F). The current temperature cycle, with a January-March low of approximately 4°C and an August-September peak of approximately 18°C, is later and less variable than before Grand Coulee Dam was closed (Jaske and Goebel 1967).

The temperature regime may favor later spawning in the Hanford Reach. During the 1960s as many as nine (in 1964) nuclear reactors were discharging thermal effluents into the Hanford Reach (Coutant 1969) and probably increasing the temperature of the Columbia River. During that time Olson et al. (1970) found that Bright eggs subjected to the warmest experimental temperatures (at increments above Hanford Reach ambient) had abnormally high mortalities just before hatching, with survivors suffering further exceptional mortalities much later at the critical first-feeding stage. The researchers did not identify a temperature tolerance ceiling, although their results (their Fig. 1, 7, 13, and 19) suggest 15°C (59°F) as the approximate limit (see also EPA 1971). Even this upper limit may be too high for best embryo viability (Combs and Burrows 1957; EPA 1971). Bright eggs spawned early in the season may be less viable because of exposure to higher water temperatures.

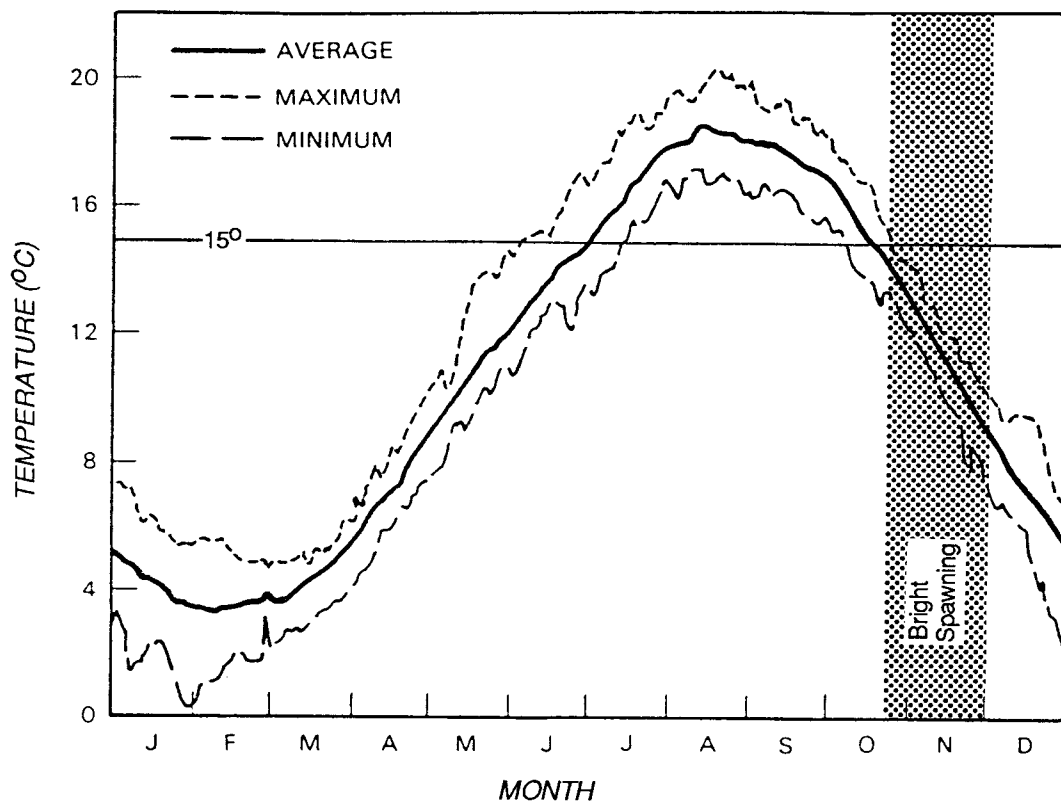


Figure 16. Period of Bright spawning in relation to water temperatures at Priest Rapids Dam. Onset of spawning corresponds with temperatures declining below about 15°C (horizontal line). Modified from Becker 1985; used with permission.

The filling of Lake Roosevelt behind Grand Coulee Dam has probably shifted the thermal window of opportunity in the Bright incubation environment. Before 1941, the Hanford Reach temperature may have fallen below the 15°C ceiling a month earlier than it presently does (mid-October; Fig. 16; Jaske and Goebel 1967). Although time of Bright egg deposition prior to 1941 is not known, it was probably earlier than at present, because temperatures declined to acceptable levels earlier in the season. Minimum winter water temperatures also are probably higher since 1941 (Jaske and Goebel 1967), which would shorten incubation time and might improve survival

to, and size at hatch (Combs and Burrows 1957; Olson et al. 1970; Beacham and Murray 1987).

Bright fry 35-40 mm (FL) long emerge from the gravel as early as March (Mains and Smith 1964; Becker 1973), and fry of this size may still be found in June (Norman 1987). The earliest emergents are apparently able to find food items, although the rapid increase in numbers of fry in shoreline feeding areas in April corresponds with a minimum in the average dry weight of stomach contents (Becker 1973). Insects -- mostly Chironomidae (midges) and a few other floating, drifting, or free-swimming autochthonous aquatic insects -- compose approximately 95% of the juvenile Bright diet (Becker 1973).

Water temperature becomes most favorable for growth in May, but during June it ascends beyond the optimum range (Fig. 17). Fish lengths are most variable during June and July (Becker 1973), when both 33-mm emergent-sized fry and 90-mm fingerlings may be present (Norman 1987). This range of sizes undoubtedly reflects broad differences in emergence timing and growth. Early emergence and rapid growth might favor survival and better growth during the relatively short May-June period of optimum growth temperatures, but adaptiveness of emergence timing has apparently not been studied.

At least one attempt has been made to estimate growth of Bright juveniles in the Hanford Reach. Norman (1987) estimated growth of approximately 0.99 mm/day based on differences between average lengths of wild coded-wire-tagged fry released in early June and recaptured in early July. Although such changes in average lengths are frequently used as growth estimates (e.g., Reimers and Loeffel 1967; Becker 1973; Reimers 1973), they probably reflect size-selective sampling methods, mortality, and emigration as well as fish growth. Good estimates of juvenile Bright growth or Hanford Reach growth conditions are lacking.

Bright juveniles are transients; "populations" in a given area are always in flux. Daily flow variations that disrupt territorial behavior, minimal shoreline habitat relative to discharge volume, and dispersed food availability may contribute to the continuous

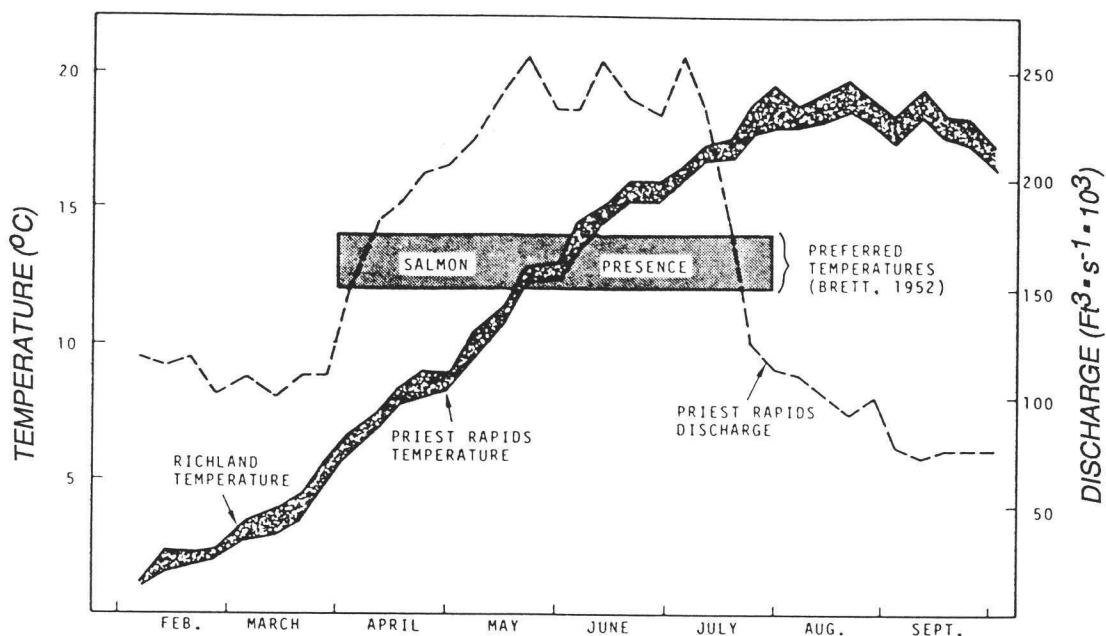


Figure 17. Columbia River temperature and flow in the vicinity of the Hanford Reach during 1969 in relation to the presence of juvenile Brights and the preferred temperatures of juvenile fall chinook salmon. Becker (1973), Fig. 2; used with permission of the author.

downstream movement of young Brights (Becker 1973). Whether movement is size related is not known. Outmigration, which generally occurs a few months after emergence during the first year of life, is considered in a later section.

As previously discussed, the larger the juveniles at time of outmigration, the better their chances for survival, continued growth, and early maturity. Juvenile size is a function of emergence time and size, growth rate, and duration of growth. Temperature, flows, and other environmental factors influencing these determinants of size have changed due to developments in the 1940s and since. Unfortunately, the limited information available provides little basis for conclusions about effects of these environmental changes on juvenile growth and size and age at maturity.

One thing is certain, too little is known about the mechanisms and potential for Bright production in the Hanford Reach. When a 1986 spawning escapement of nearly twice the management escapement goal produces "a large healthy 1987 presmolt wild fall chinook rearing population in the Hanford reach," (Norman 1987, p. 15), the rationale for the escapement goal must be questioned; it may be too low. Others have also challenged the basis for the escapement goal (Rogers and Hilborn 1988).

Priest Rapids Hatchery Environment

Introduction Hatchery practices can directly influence size and age at maturity in the propagated stocks in at least two principal ways, through mating procedures and rearing practices. Bright broodstock acquisition and spawning practices at Priest Rapids Hatchery are addressed in a later section; rearing practices are of interest here. Does the rearing environment at Priest Rapids Hatchery contribute to lower size and age at maturity? I tested the null hypothesis that Brights produced by Priest Rapids Hatchery mature at the same age as those produced naturally in the Hanford Reach.

Releasing large smolts has become a norm for Columbia River hatcheries that raise anadromous Pacific salmon (Wallis 1968; Seidel et al. undated). As discussed previously, this practice achieves a higher survival rate, but can also lead to undesirably early maturity. Still, survival rate (regardless of sex composition and size at return) apparently continues to be the favored measure of hatchery performance (Seidel et al. undated, 1988).

Priest Rapids Hatchery began operation as a spawning channel in 1963 to mitigate for Bright spawning habitat lost when Priest Rapids and Wanapum dams were constructed. Designed to accommodate 2,500 pairs of spawners in a 6000-ft (1969 m) long channel, the facility was beset by high mortalities and low adult returns during its first decade (Allen and Meekin 1973). Artificial spawning and incubation began in 1972, and since 1978 the spawning channel has been used

exclusively for conventional raceway rearing (M. Dell, Public Utility District No. 2 of Grant County, WA, pers. comm., 8/88).

Since the spawning channel concept was abandoned, Priest Rapids Hatchery has released Bright juveniles that are much larger than the naturally produced Brights residing at the same time in the Hanford Reach. Allen and Meekin (1973) recommend release of fingerlings at approximately 80 mm (about $75 \cdot \text{lb}^{-1}$), and others have recommended rearing to a size of $40 \cdot \text{lb}^{-1}$ (Kaczynski and Moos 1979). Fingerling releases since 1978 have generally been at sizes of $50\text{-}100 \cdot \text{lb}^{-1}$ (unpubl. data provided by M. Dell, Public Utility District No. 2 of Grant County, WA), and those released in 1987 (June 6-18) averaged $60\text{-}74 \cdot \text{lb}^{-1}$ and 82-90 mm long (unpubl. data provided by G. Osborne, WDF, Manager, Rocky Reach Hatchery)³. This contrasts with naturally produced fingerlings seined from the Hanford Reach on June 9, 1987, which averaged only 57.0 mm in length (Norman 1987).

Incubation in 11.7°C (53°F) well water at Priest Rapids Hatchery accelerates embryonic development, permitting a longer period of feeding and growth prior to release. Fry hatch in December and are ponded (when feeding starts) from the last week of January through the third week of February. Ponded fry have in the past enjoyed 10°C (50°F) environments and rations of $\leq 4\%$ of body weight per day while the unemerged and perhaps unhatched natural fry are exposed to the 4°C winter waters of the Hanford Reach. As the hatchery fry grow, Columbia River water at ambient temperature supplants the well water. Growth is regulated through temperature and diet to attain 100,000-120,000 lb of total production for mid-June release (Paul Pedersen, Manager, Priest Rapids Hatchery, pers. comm.). Can this prolonged period of favorable growth, which results in such large size at release, cause the fish to mature earlier?

³ Length at release for Brights from Priest Rapids Hatchery reported by Howell et al. (1985a; 100-130 mm) and cited by Mullan (1987) appears to be inconsistently high for the reported number of fish per pound (60-100) and the data available from other sources.

Methods Mean ages, lengths, and sex compositions (percent female) of known hatchery-produced spawners were compared, for return years 1980-87, with spawners presumably produced naturally in the Hanford Reach. Recoveries of Priest Rapids Hatchery CWT codes (Appendix C) in the Hanford Reach spawning ground surveys, at Priest Rapids Hatchery, and in spawning ground surveys above Priest Rapids Dam represented fish of Priest Rapids Hatchery origin (unpubl. data provided by S. Markey, WDF, Olympia, WA). Over 95% of the CWT recoveries were from Priest Rapids Hatchery.

Bright fingerlings produced naturally in the Hanford Reach have been coded wire tagged only since 1987 (1986 brood, first returns as jacks in 1988; Norman 1987), so natural fish could not be positively identified during the return years examined. Biological samples taken during spawning ground surveys in the Hanford Reach by personnel from WDF's Columbia River Laboratory, Battle Ground, WA, were used, with some modification, to represent naturally produced fish. For the 1985-87 returns, spawners bearing CWT codes from any hatchery were eliminated from the data set. Because most of the coded wire tagged fish were from representative tag groups in a larger release (i.e., only a fraction of the release group was tagged), enough fish of the same sex, age, and length (as each CWT-bearing fish) were also eliminated to account for untagged fish in the hatchery release that could be expected in the spawning ground survey samples. For 1985-87, less than 5% of the records were eliminated as known hatchery (coded wire tagged) or as being representative of untagged hatchery fish.

Not all hatchery-produced fish could be identified and eliminated, but this failure only makes observed differences more conservative. In many years, substantial proportions (approximately 80% for 1983-85 releases) of the hatchery Bright releases in and above the Hanford Reach were not represented by CWT groups (Coleman and Rasch 1981; Castoldi and Rasch 1982; Castoldi 1983; Hill 1984; Kirby 1985; Abrahamson 1986; PMFC 1988). Additionally, spawning ground survey data for 1980-84 -- obtained largely in computerized form from the National Marine Fisheries Service, Portland, OR (R.

Vreeland) -- did not identify tagged fish, so no hatchery fish were eliminated from the data for 1980-84. Hence, data from spawning ground surveys that were used to represent natural fish in all years contained an unknown, but probably minor proportion of hatchery-produced fish. In 1979-82, as many as 8% to 33% of the spawners on Vernita Bar (a heavily used spawning area near Priest Rapids Hatchery) and elsewhere in the Hanford Reach may have originated in hatcheries (Chapman et al. 1983 cited in Becker 1985; other sources cited in Dauble and Watson 1990). Norman (1984) estimated that only 8.7% of the fish spawning naturally in the entire Hanford Reach in 1983 were of Priest Rapids Hatchery origin. The effect of this "contamination" would be to reduce the apparent differences between the two groups and make resulting conclusions more conservative.

Scale samples taken from Bright carcasses during the spawning ground surveys were analyzed by WDF personnel to determine age. Only records for which an age was recorded were included in these analyses.

No statistical tests of significance were attempted between hatchery and natural groups within each year, because of potentially large biases in the data. For example, returns of Priest Rapids Hatchery fish in a given year are of five age classes (2-6), and the distribution among the classes is a function of at least three extraneous factors in addition to the inherent age distribution:

- 1) numbers of tags released for each of the several broods represented in the run,
- 2) fingerling-to-adult survival for the broods, and
- 3) proportion of, and selection criteria for Priest Rapids Hatchery brood stock trapped at Priest Rapids Dam (large fish and females are generally selected). (This selection also represents a potential bias, which will be discussed later.)

Differences in these factors among broods and return years can affect the real and apparent age distributions of returning hatchery fish. Similarly, differences in production and survival of broods distort expression of the inherent age distribution for natural fish.

Numbers of tags released for the hatchery broods are known and corrections could be made for the differences in numbers of tags among releases, but differences in natural production, survival of both groups, and broodstock selection during dam trapping are not known. These biases, which influence values (i.e., mean age, mean length, and percent female) for the two groups, may act independently and could be sufficiently large to render tests of significance for single year comparisons meaningless.

Annual means of length and age for each sex, as well as percent female for all years (1980-87) were evaluated with the sign test for the null hypothesis that the values for hatchery and natural fish were equal. Generally, the mean values within a treatment and among years are sufficiently independent that the outcomes between treatments within years are not influenced by the results of prior years. Graphical comparisons were made using ratios of mean length-at-age to illuminate potential differences in growth and maturity patterns.

Results For the years 1980 through 1987 the returning hatchery fish were shorter, were younger, and had a lower percentage of females in nearly all years (Table 1 and Appendix D). The differences were generally, but not consistently, less for females (higher ratios in Appendix D) than for males. Only for male length (both for all ages and ages 3-6 comparisons) and percent female (all ages) were differences sufficiently consistent among years to be statistically significant (sign test; $P \leq 0.01$). Including jacks (all ages) or excluding jacks (ages 3-6) made little difference in the outcomes (Table 1).

There are no striking patterns in the ratios of mean length at age, although negative slopes are common (Fig. 18). Negative slopes indicate that hatchery fish become smaller, relative to their natural counterparts, with increasing age. Any potential size (growth) advantage associated with hatchery rearing, which is not clearly demonstrated in Fig. 18, is expressed more in younger age classes.

Table 1. Summary of length, age, and sex composition of hatchery and natural spawners returning in 1980-87. Means and percent female are unweighted averages of the eight annual observations. Probabilities (P) are from the sign test (two-tailed, cumulative for observed distribution plus more extreme distributions), which compared hatchery and natural values for each year to test the H_0 that the overall hatchery value = overall natural value. ** = significant at $P \leq 0.01$. Detailed data are in Appendix D.

	<u>Mean</u>		No. of Years (of 8) when Mean <u>is Greater for:</u>		P
	Hatchery	Natural	Hatchery	Natural	
<u>All Ages</u>					
Males: Length (mm)	700	748	0	8	0.008 **
Age (yr)	3.21	3.36	1	7	0.07
Females: Length (mm)	858	888	2	6	0.29
Age (yr)	4.05	4.24	2	6	0.29
Percent Female:	40.8	49.8	0	8	0.008 **
<u>Ages 3-6</u>					
Males: Length (mm)	764	823	0	8	0.008 **
Age (yr)	3.52	3.70	1	7	0.07
Females: Length (mm)	858	890	2	6	0.29
Age (yr)	4.05	4.25	2	6	0.29
Percent Female:	46.6	55.4	1	7	0.07

Such a trend is expected under the hypotheses that favorable early growth hastens maturity and that this effect is expressed most clearly in individuals genetically predisposed to early maturity.

The results of the comparisons of mean age, mean length, and percent female are consistent among themselves. As would be expected, earlier maturity in the hatchery group is associated with lower mean lengths and lower percentages of females (males prevail at ages 2 and 3 and may be more "elastic" in their age at maturity).

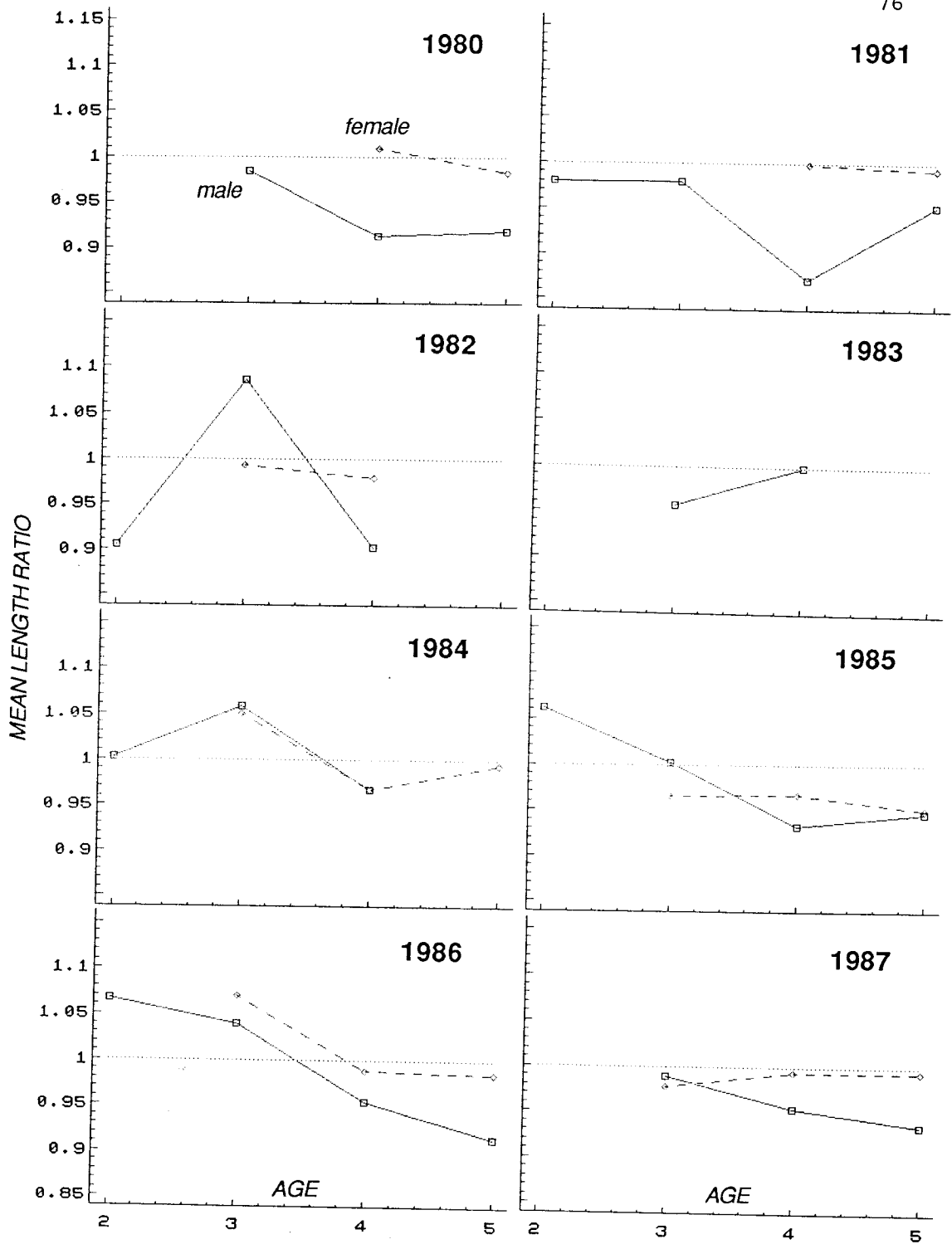


Figure 18. Ratios of mean length at age of Bright hatchery and natural spawners returning in years 1980-87. Ratios are derived by dividing hatchery mean length by natural mean length; hence, values less than unity (horizontal dotted line) indicate the hatchery value is the lesser. See Appendix D and text for data details.

The lower proportion of females and their smaller size in the returns of hatchery fish indicate that hatchery fish probably have lower reproductive potential on a per-fish basis (both sexes and all ages) than the returning natural fish. This can be coarsely quantified using a fecundity-length regression and a ratio of percent female. The equation,

$$F = 9.853L - 3484$$

where F is fecundity and L is FL (mm), was derived for Bright spawners in 1983, 1985, and 1986 from the egg bank at Bonneville Hatchery (unpubl. data provided by D. Hankin, Humboldt State University, Arcata, CA). The coefficients in this equation are within the broad range of coefficients calculated for Bright spawners at McNary, Priest Rapids, and Rocky Reach spawning channels (Mathews and Meekin 1971). Estimated fecundities were calculated for all hatchery and natural females in the samples. The average estimated fecundity (all years and all ages combined) of hatchery females, because of their generally smaller size, was 96% of that estimated for natural females (Appendix Table D.6). The proportion of females in the returning hatchery fish was only 82% (40.8/49.8, from Table 1) that of the returning natural fish. Hence, the reproductive potential of the hatchery fish sampled in the escapement was only about 79% ($0.96 \cdot 0.82 \cdot 100$) as great as the natural fish sampled. Most of this difference is a result of the lesser proportion of females in the hatchery samples.

Discussion This analysis suggests that Brights produced and coded wire tagged at Priest Rapids Hatchery and returning during 1980-87 were younger, smaller, and more likely to be male than their natural counterparts from the Hanford Reach. Therefore, the average hatchery fish in the escapement may not be the equal of a natural fish in reproductive potential. This does not take into account potential differences in spawning success and viability of progeny. Although it could not be shown statistically that Brights from Priest Rapids Hatchery mature earlier than their natural counterparts,

statistically significant differences were found in lengths of males, and sex composition, and females were proportionately fewer among escaping hatchery fish than among natural fish. Potential sources of bias exist that could have influenced, positively or negatively, the differences found in these results.

Aging of Bright scales tends to be biased slightly downward (Roler et al. 1984; LeFleur and Roler 1985), perhaps due to resorption of the scale margins and resulting loss of annuli. Such bias could cause the mean estimated ages of the presumed natural fish used in this analysis to be lower than means of true ages. The true differences between mean ages of the two groups may therefore be greater than indicated here. Ages of hatchery fish are determined from CWT codes and are not likely to be biased, although the age composition in a given year may be biased for other reasons.

Carcasses sampled on the spawning ground surveys may not be accurately sexed, although the net effect of misidentifying the sex of the fish on differences in reproductive potential, as calculated here, is probably negligible. Fish of smaller sizes, whose external morphology differs little or not at all between sexes, may be the greatest source of error. For example, in 1984, 44 (8.5%) of the 516 2-yr-olds sampled were identified as females, but in the subsequent 3 yr none of the 422 total 2-yr-olds were identified as females. Currently, the proportion of 2-yr-old females is assumed to be negligible (even 3-yr-old females are few), and all jack-size carcasses are automatically designated as male (personal observation). This assumption, which is probably correct, apparently did not prevail during 1984, and it is likely that most or all of the 44 2-yr-olds reported as female were actually males. This probable misclassification would cause the 1984 natural female mean age and length to be too low, those of males to be too high, and the percent female to be too high. The 2-yr-old "females" in 1984 also reduced the estimated fecundity of the natural females (Appendix Table D.6). The small overall effect of this misidentification is to make the differences appear smaller than they actually are.

It may not be accurate to assume that hatchery and natural females have the same length-fecundity relationship. Rapid freshwater development, as would occur in a hatchery environment, has been associated with higher fecundity (but smaller egg size) at a given body size in Atlantic salmon (Thorpe et al. 1984). A similar phenomenon may occur in Brights.

Potentially serious and unrecognized biases may be associated with the two different sources of the data. Samples of returning hatchery fish came overwhelmingly from Priest Rapids Hatchery itself, either from spawners voluntarily entering the discharge stream (hereafter, "volunteers") or from brood stock trapped at Priest Rapids Dam (hereafter, "conscripts") just upstream from the hatchery.

Conscripts are intentionally unrepresentative of the run; hatchery personnel selected the larger fish, and the proportion of brood stock obtained by this method (Fig. 19) and the selection criteria often vary from year to year (Allen and Meekin 1973; Bruce Ault, WDF, Soleduck Hatchery, pers. comm.). An upward bias in mean age of the hatchery fish could be expected, depending on how much of the brood stock was obtained from the dam trap and how intense the selection was during the 8-yr period. This potential bias would make the differences appear smaller than they really are.

The volunteers to Priest Rapids Hatchery, which contributed substantially to the data set of hatchery-produced fish, may be smaller and younger on average than the population of returning hatchery fish. The hatchery discharge stream, which flows through an excavated ditch from the end of the former spawning channel to the Columbia River, is shallow and miniscule compared to the river channel. It is possible that large spawners may prefer to remain in the deep, broad mainstem. Large fish (> 20 lb) are believed to avoid using shallow overflow entrances to fishways (Bell 1986). Jacks were especially prevalent among the Bright volunteers at the McNary Spawning Channel discharge stream (Meekin and Harris undated, 1967), suggesting a greater attraction to smaller fish. Jacks have also been abundant among the volunteers to Priest Rapids Hatchery (Fig. 20), but it is not known whether their proportions are exceptional

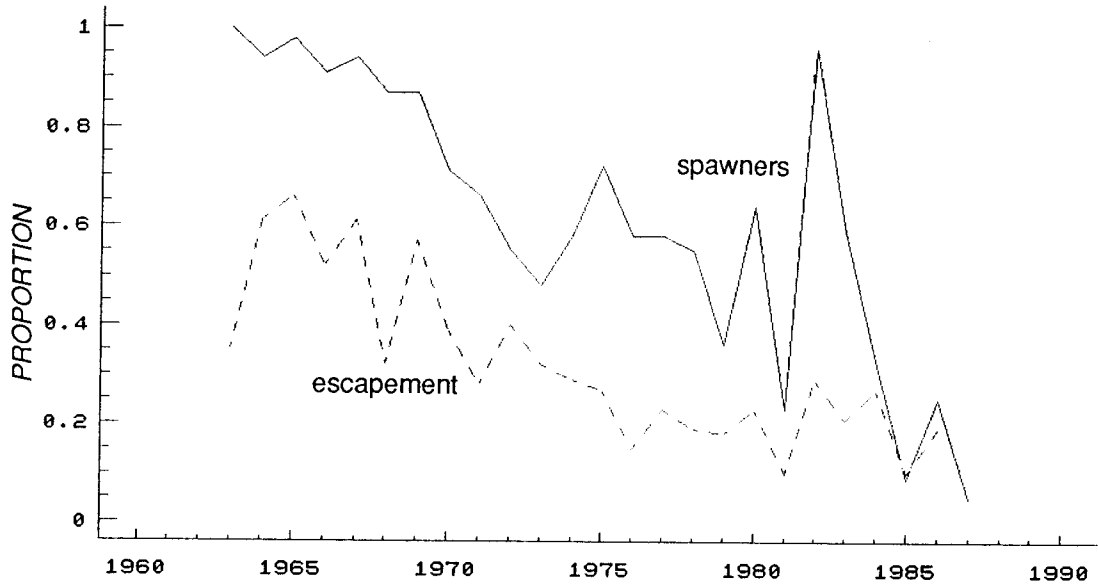


Figure 19. Proportion of adult brood stock for Priest Rapids Hatchery that was trapped at Priest Rapids Dam (solid line) and the proportion of adult Brights passing Priest Rapids Dam that was removed for use as brood stock at the hatchery (dashed line). Data provided by M. Dell, Public Utility District No. 2 of Grant County, Ephrata, WA.

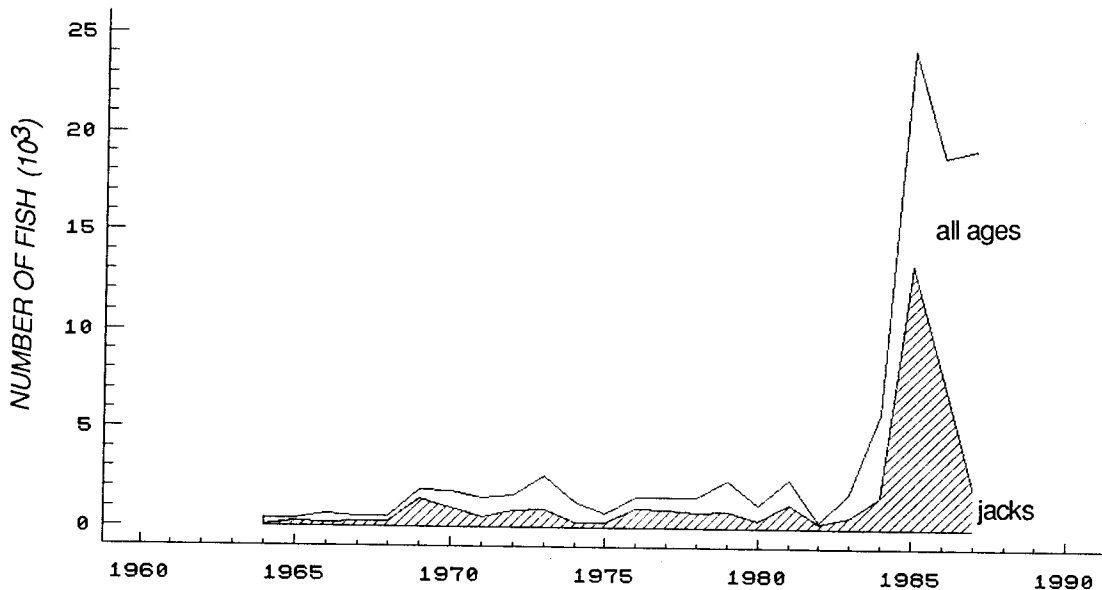


Figure 20. Numbers of jacks and Brights of all ages that voluntarily entered the Priest Rapids Spawning Channel trap, 1964-87. Data provided by M. Dell, Public Utility District No. 2 of Grant County, Ephrata, WA.

relative to the entire run of hatchery fish. Insufficient numbers of tagged fish have been recovered from the Hanford Reach to test for differences between those that remain in the river to spawn and those that voluntarily return to the hatchery. Biases in size and/or sex associated with volunteers to the hatchery, if real, would cause the differences noted here to be exaggerations; they would also cause data collected from volunteers at Priest Rapids Hatchery to be unrepresentative of the run.

Likewise, carcasses sampled on the spawning ground surveys may not be totally representative of the Brights spawning naturally in the Hanford Reach. Factors associated with size and sex may influence which carcasses are washed ashore, come to rest in shallow waters, or otherwise become available to sampling. Of the estimated numbers of spawners in the Hanford Reach in 1983-87, less than 6% were encountered during spawning ground surveys (from estimates and data in Roler et al. 1984; LeFleur and Roler 1985; Roler and LeFleur 1986; Roler 1987, 1988). Can it be assumed that those 6% or less found along the shorelines have the same size and sex compositions as the remaining 94% that are caught-up on submerged boulders and debris (Swan et al. 1988) or are otherwise unavailable to samplers? Perhaps not.

Oregon Department of Fish and Wildlife (ODFW) studies on fall chinook salmon in the small coastal Salmon River suggest that in some years males and the smaller fish of both sexes are recovered at lower rates by the spawning ground surveys than they occur in the run (Boechler and Jacobs 1987; unpubl. data provided by S. Jacobs, ODFW, Corvallis, OR). Differences in postreproductive behavior between the sexes and removal of small carcasses by scavengers have been hypothesized as possible reasons. Although the results from the Salmon River cannot be extrapolated to the Hanford Reach, we also cannot assume that Hanford Reach samples are always good indicators of the naturally spawning Bright population. A majority of spawning in the Hanford Reach may occur in very deep water (Swan 1989), and it is questionable whether the fish that spawn there are adequately represented in the spawning ground samples. Males and small fish may

be under (or over) represented in the spawning ground survey data, possibly contributing to (or detracting from) the apparent differences between hatchery and natural fish.

Considering the potential biases, the apparent reproductive inferiority of hatchery-produced fish can be interpreted in two ways: (1) as a real difference, meaning hatchery fish have substantially lower reproductive potential and are not representative of the run as a whole (including natural fish), or (2) as a spurious result of sampling biases, meaning that one or both sources of escapement data (CWT recoveries and spawning ground surveys) may be biased. Both interpretations may be correct in part, and neither can be ruled out. However, available evidence suggests that something about hatchery rearing, probably favorable growth conditions, tends to reduce age at maturity and contribute to a high proportion of males in the returns. Atlantic salmon are expected to develop more rapidly and mature earlier when exposed to practices similar to those used at Priest Rapids Hatchery (Ritter et al. 1986; Saunders 1986; Thorpe 1986). For chinook salmon, age-specific maturation probabilities are believed by some to be strongly influenced by hatchery rearing and release practices (Hankin and Healey 1986). It is reasonable to suspect that rearing practices at Priest Rapids Hatchery contributed to real differences in age (and size) at maturity that were manifest in the comparison with natural spawners.

Changes in age at maturity caused by hatchery rearing practices (e.g., rapid early growth) are probably phenotypic and do not necessarily lead to genetic changes in the stock (Fig. 1.D; see also *Growth and Age at Maturity*, p. 59). However, there is one relatively obvious way that hatchery practices can indirectly result in genetic selection for size and age. Hatchery stocks that have higher lifetime survival can support higher harvest rates in fisheries. Survival benefits obtained in the spawning, incubation, and early rearing stages can be passed on to fisheries as higher harvest rates. If those fisheries are selective, then the increased harvest rate made possible by hatchery operations can intensify selection in the fishery. Selection intensity is a function of degree of selection

and proportion of the population impacted by selection (Appendix B; see also Role of Stock Abundance, p. 173).

Summary and Conclusion This section examined the Priest Rapids Hatchery environment to determine if incubation and juvenile rearing practices could have contributed to declining size in the run. Conditions at Priest Rapids Hatchery are favorable for rapid development and growth; size at release has been greater than the concurrent size of natural fingerlings in the Hanford Reach. Good growth conditions are known to hasten maturity (Alm 1959; Wallis 1968; Lorz 1971; and other sources cited in *Growth and Age at Maturity*, p. 59).

Known hatchery Brights in the 1980-87 escapements were generally younger, smaller, and less likely to be female than presumedly natural Brights sampled during spawning ground surveys. The differences are probably real, at least in part, meaning that returning hatchery fish may have lower reproductive potential than their natural counterparts (0.79 was the calculated ratio of reproductive values, with all ages and years combined). Known and potential biases in the data could have influenced, positively or negatively, the apparent differences. Such biases, if real, would make escapement data from these two sources unsuitable for many analyses. In either respect, it appears that CWT recoveries from Priest Rapids Hatchery are not representative of the natural spawners and hence the Bright run as a whole.

I conclude that rearing practices at Priest Rapids Hatchery probably contribute to reduced size at maturity in Brights produced at the facility. The sex composition of the returning hatchery fish also appears to be influenced. Increased hatchery production and a greater emphasis on large size at release during the last three decades has very likely contributed in an unknown degree to the observed declines in age and size at maturity in the run as a whole. Brights, even now managed principally as a hatchery stock (Rogers and Hilborn 1988), can be expected to show a greater tendency toward early maturity as artificial propagation contributes greater portions

of the run and as long as maximizing survival remains an emphasis in artificial propagation programs.

As suggested by Johnson (1970) and Bilton et al. (1982), reproductive and commercial value would be more appropriate gauges for evaluating hatchery programs than mere survival. Numbers of fish alone may not reveal potential problems with the quality (e.g., size, sex composition) of those fish.

Early Rearing Summary

Factors in the early life environment can influence, particularly through maternal influences and growth conditions, the size and age of spawners. Temperatures, flows, and probably other factors in the Hanford Reach environment have changed dramatically since the 1940s, but how those changes have affected the relative fitnesses of large and small female spawners and influenced juvenile growth remains uncertain. Small females and their progeny may not be as disadvantaged by present spawning and incubation conditions relative to past conditions. Present conditions may also be more favorable for juvenile growth, which can reduce age at maturity. Disappointingly little is known about the productive mechanisms and capacities of the Hanford Reach environment; even less is known about how the environment selects for spawner size and influences juvenile growth.

Data were available, however, to take a first look at how rearing conditions at Priest Rapids Hatchery may have contributed to the declines in size and age. Spawners returning to Priest Rapids Hatchery are smaller and less likely to be female than are Brights sampled in the natural spawning areas of the Hanford Reach. These differences, which indicate that the hatchery fish have less reproductive potential per fish, are an expected result of accelerated development of juveniles in the hatchery. The differences may also result in part from sampling biases that would reduce the accuracy and usefulness of data collected from Priest Rapids Hatchery and spawning ground surveys in the Hanford Reach.

Increased hatchery production and increased size at release have probably contributed to declining size at maturity in the run.

Outmigration

Formerly a free-flowing conduit for outmigrating Brights, the mainstem Columbia River between the Hanford Reach and Bonneville Dam is now a chain of four dams and reservoirs. Turbine-caused mortalities are estimated at 10-30% per dam (NPPC 1987), and total passage mortalities may be 35-51% per dam/reservoir project (based on 6-18% survival of juveniles released at Ringold Ponds relative to juveniles transported to below Bonneville Dam in 1968-69; Dawley et al. 1986). Ameliorating the large dam- and reservoir-related mortalities to juvenile outmigrants is probably the most pressing and controversial problem facing fishery managers on the Columbia. I examined these mortalities to determine how, if at all, they might be selective for traits related to size and age in the adult run. Good relevant information is scant; hence, this coverage will be brief and largely conjectural.

The outmigration pathway is a virtual gauntlet of dams and reservoirs. Downstream movement of newly emerged fry in the Hanford Reach has been known to begin in March and peak in April, with larger fingerlings outmigrating at least into July (Edson 1957; Mains and Smith 1964). In recent years, Brights and other subyearling chinook salmon outmigrants have passed McNary Dam, the nearest downstream project (Fig. 3), during relatively short periods principally during June and July, with smaller numbers passing during late summer and fall months (Karr and DeHart 1986; DeHart and Karr 1987, 1988) (Fig. 21). The present contracted migration period may be the result of selective forces imposed by in-river developments.

Turbines and predators are important causes of outmigrant mortalities associated with dams and reservoirs. Since 1972, the mainstem dams have had the generating capacity to pass essentially all of the Columbia's flow (and outmigrating Brights) through turbines (Park 1985). At least one study has suggested that turbine mortality may be a function of fish size (Cramer and Oligher 1964),

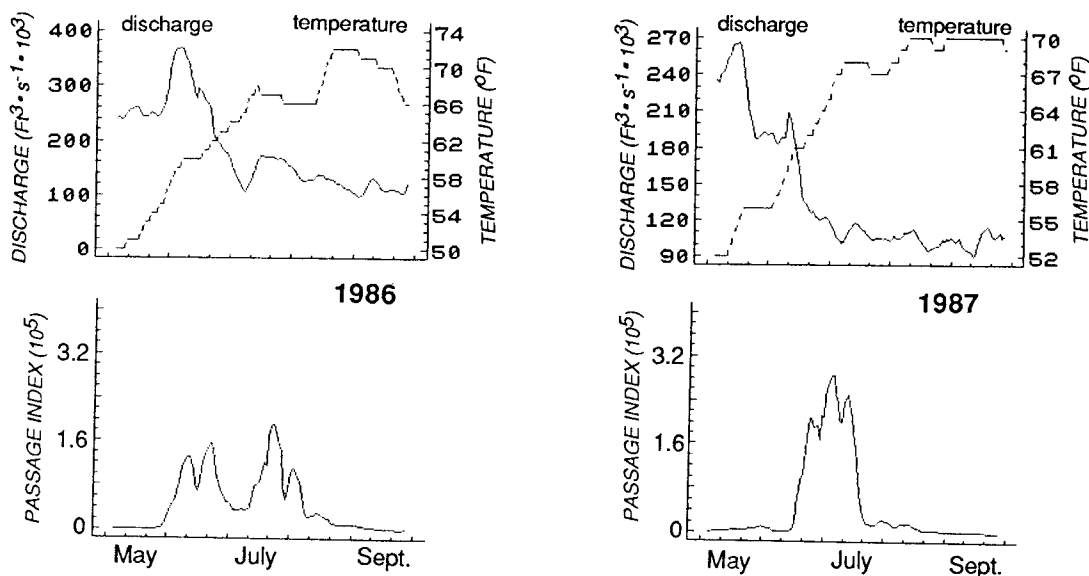


Figure 21. Passage of outmigrating subyearling chinook salmon (mostly Brights) at McNary Dam in association with discharge (river flow) and water temperatures, 1986 and 1987. All points represent 7-d moving averages. The passage index is assumed by some to be proportional to the number of juveniles passing the dam (DeHart and Karr 1988). Data from the Fish Passage Center, Portland, OR.

but differential mortality over the size range of outmigrating Brights is not likely to be great. McNary Dam's highly regarded mechanical bypass system (NPPC 1987) is estimated to divert less than 50% of subyearling chinook salmon around turbines under the best conditions (0.65 maximum theoretical fish guiding efficiency times 0.75 submersible travelling screen effectiveness, Brege et al. 1988, pp. 17-19). At McNary Dam, fish that are not guided must negotiate the lower three dams and reservoirs, as well. Brights collected in the bypass system at McNary Dam are usually transported by truck and barge past the downstream dams and released below Bonneville Dam. High temperatures associated with low flows during the latter part of the subyearling outmigration apparently contribute to the poor bypass efficiency at McNary Dam (Brege et al. 1988) and to direct mortalities (Koski et al. 1988).

Flows are controlled by the U.S. Army Corps of Engineers, although the tribes and fishery agencies may request a small volume of water (known as the Water Budget) to assist the passage of spring migrants between 15 April and 15 June (DeHart and Karr 1989). Because most Brights migrate later, in the summer, very few benefit from the Water Budget, and most suffer from it because of energy storage accounts that reduce flows in the summer to compensate for Water Budget use in the spring (DeHart and Karr 1989, 1990). Low flows increase the time required for smolts to pass through the reservoirs (DeHart and Karr 1990), thereby increasing exposure to predators.

Increased predation by northern squawfish (*Ptychocheilus oregonensis*) and other predators on subyearling migrants passing McNary Dam is associated with increased temperatures and reduced flows during July and August (Vigg et al. 1988; Rieman et al. 1988). Dam passage mortalities and predation appear to select for earlier Bright outmigration. But, earlier (smaller) outmigrants may be vulnerable to a greater size range of predators (Poe et al. 1988), so predation may also select for larger size at outmigration. (Recall that predation is the favored hypothesis to explain the association between juvenile growth and survival.) Predation by mainstem reservoir fishes provides a plausible explanation for the relative paucity of young, early migrants and the contracted period of subyearling passage at McNary Dam (Koski et al. 1988). If predation and/or other factors in the outmigration environment select for early migration at large size, then they select for rapid growth. Rapidly growing juveniles also are more likely to mature early.

In addition to harboring hundreds of thousands of predatory fish (Beamesderfer and Rieman 1988), the mainstem reservoirs may also be rearing environments for small Brights (Miller and Sims 1984; Becker 1985; Rondorf et al. 1990). Whether reservoirs represent better growing environments than the free-flowing stretches they replaced is certainly open to debate, as is the net benefit (perhaps negative) to the population of reservoir rearing when predation rates are high. Like other size-selective factors, intense predation may

allow only the largest and fastest growing individuals to survive, thereby reducing stock abundance while at the same time promoting reduced age and size at maturity. This may be occurring.

The Columbia River estuary is more than simply a portal into the marine rearing environment. The importance of estuaries for growth of some subyearling chinook salmon was recognized as early as the 1920s (Rich 1922) and is now widely accepted (reviews by Fraser et al. 1982; Levy 1984; Simenstad and Wissmar 1984). Outmigrating Brights continue to share the Columbia River estuary with tens of millions of other subyearling chinook salmon (Bottom et al. 1984), but only recently has their use of the estuary been investigated in any detail.

Although subyearlings typically linger in shallow nearshore estuarine areas feeding on zooplankton and insects, large hatchery Brights may use more mid-channel areas while passing quickly through the estuary (Bottom et al. 1984; Dawley et al. 1986). Natural Brights could not be identified during these studies, so their use of the estuary is not known. Because of their smaller size, they may rely more heavily on the estuary for rearing than their larger hatchery counterparts.

Subyearling consumption rates in the Columbia River estuary may be low relative to those in other locales, perhaps because of limited food availability (Bottom et al. 1984), or because many are actively migrating rather than foraging (Dawley et al. 1986). Large areas of productive wetlands have been lost in the estuary during the last century (Simenstad et al. 1984), and the annual freshets that formerly expanded the estuary during the juvenile outmigration have been controlled. Also, subyearling densities may have increased with massive production of hatchery fall chinook salmon. Estuary conditions may limit, to an unknown degree, the growth and survival of outmigrating Brights.

To summarize, whether a Bright avoids the myriad causes of death and continues to grow during its outmigration is a function of many behavioral as well as physical factors. A few of the factors -- such as time of migration, size, and water temperature -- can be

identified, but how they interrelate and affect traits at maturity is not clearly understood.

This section dealt just briefly with these more obvious factors, not to demonstrate that they are influential in determining adult size and age, but to illustrate the potential for influence. Outmigrant mortality rates are extremely high and their consequences are perhaps more severe than adult mortalities of similar magnitude (Junge 1970). In this case the principal objective of fishery managers should be, and is, to moderate the mortalities, not to determine how they influence size and age at maturity.

Ocean

Although still somewhat of a "black box," the ocean environment in which Brights rear for 1-5 yr is acquiring some definition. More is being learned about how ocean growth conditions, natural mortalities, and harvests relate to size and age of the fish.

Natural Environment

Brights enter the marine environment at a vulnerable stage in an area of the Northeast Pacific Ocean that is not always hospitable. They are no doubt subject to the annual variability in coastal upwelling that is associated with early-ocean survival of yearling coho salmon smolts in the Oregon Production Index area (Nickelson 1986). Other anadromous salmonids are also sensitive to physical conditions early in their marine existence. Survival and perhaps age at maturity of Icelandic Atlantic salmon are related to marine physical factors and feeding conditions during their smolt year (Scarnecchia 1983, 1984a,b; Scarnecchia et al. 1989). Good growth during the first marine year also has been associated with higher proportions of sockeye salmon maturing after a single ocean season (Killick and Clemens 1963). Throughout marine life, growth probably continues to influence survival and age at maturity (Gilbert 1924; review by Wallis 1968), but there is little evidence pertaining directly to Brights.

Although young chinook salmon of some stocks with subyearling life histories apparently rear near the mouth of the Columbia River (Rich 1925; Wright et al. 1972), Brights are known to rear in distant areas off of Southeast Alaska (Fig. 22) (Parker and Kirkness 1956; Funk 1981). The extent of the stock's marine range has not been well defined, as CWTs are recovered only where monitored fisheries occur. A stock may show a high degree of fidelity for a particular area, as

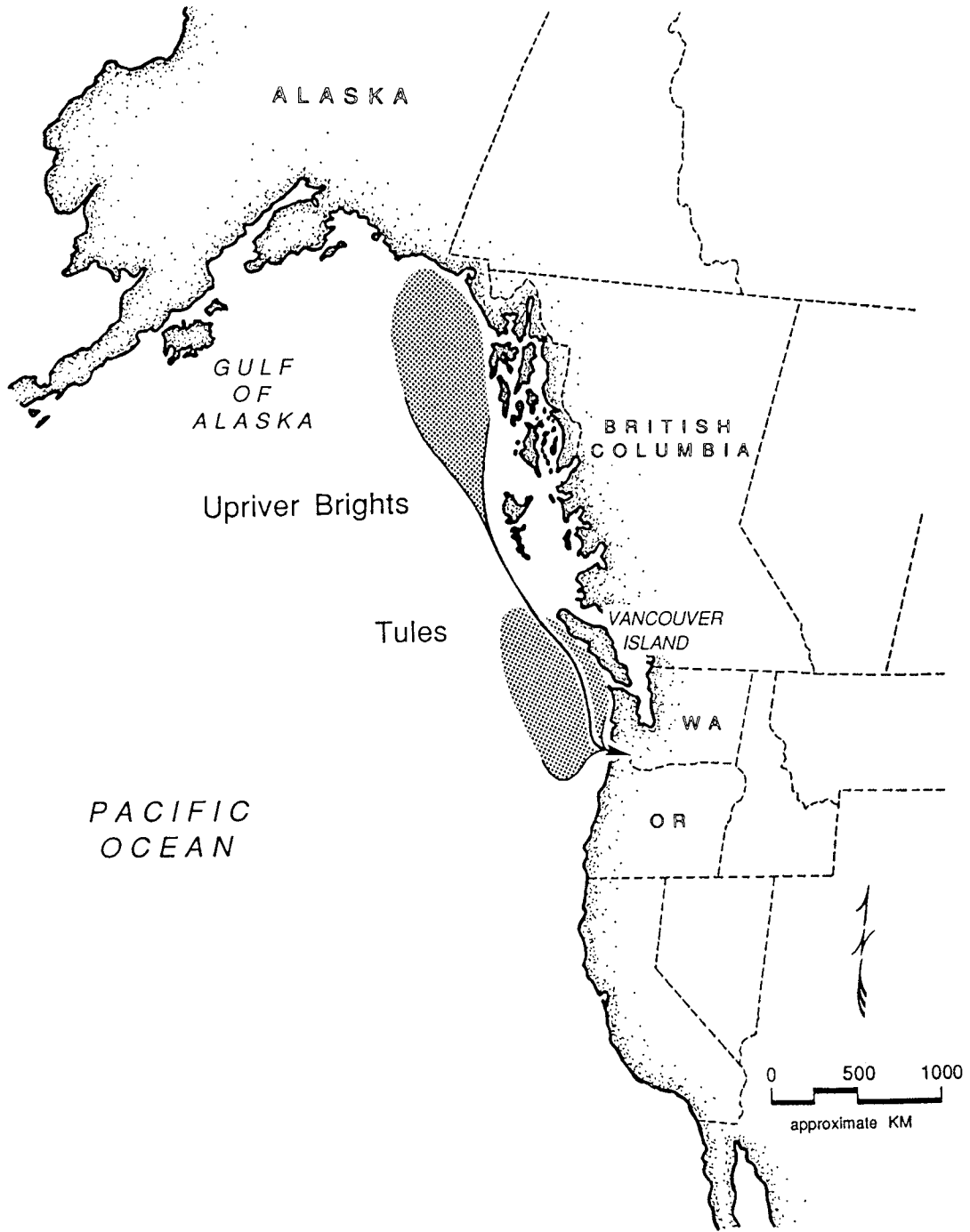


Figure 22. Generalized known ocean rearing areas of Brights and tule fall chinook salmon from the Columbia River.

suggested by the almost total loss of chinook salmon catches in a formerly highly productive trolling area of Southeast Alaska (Parker and Kirkness 1956). Parker and Kirkness (1956) speculated that the failed productivity of many of these trolling grounds was attributable to the destruction of spawning grounds in the Columbia River, an attribution that links stocks to specific marine rearing areas.

As perhaps first noted by Van Hyning (1973), there appears to be a clear separation between the distributions of Columbia River tule fall chinook salmon, which rear primarily off Washington and southern British Columbia, and Brights, which rear mostly far to the north. Those Brights taken by British Columbia and more southerly fisheries (Howell et al. 1985a) are probably on their spawning migration, although this has not been proved. The distinction between rearing areas, as well as other differences between the two stocks, is significant for interpreting the relevance of some size and age trends in fisheries (e.g., Milne 1957; Miller 1977) for this study. For example, trends in sizes or ages of Brights in British Columbia troll fisheries are more likely to reflect changes in size and age at maturity (assuming that the fishery takes mostly maturing Brights) than are similar data from the Southeast Alaska troll fishery (assuming that a large proportion of the Brights caught would not mature in the year of catch). Also, Brights and tules probably encounter very different marine environments, including fisheries, so generalizations probably cannot be made between the two stocks.

Evidence for density dependent marine growth and survival of Pacific salmon suggests that for some stocks food availability may sometimes be limited (Peterman 1980, 1984; Eggers et al. 1984; McGie 1984). Chinook salmon have long been recognized as opportunistic feeders in the ocean, feeding "on anchovies, herring, smelts, sand launces (*sic*), shrimps, and in general on any living thing," (Stone 1884, p. 480). Such a general and variable diet (see also Williamson 1927; Chapman 1936; Pritchard and Tester 1939, 1941, 1942) indicates that feeding conditions depend not so much on abundance of a particular type of prey as on overall ocean productivity.

Productivity in the Northeast Gulf of Alaska, where Brights rear, is strongly influenced by large-scale processes. Unlike the southern areas from California to British Columbia, where nutrients may be limiting and seasonal production is dependent on intermittent upwelling, production cycles in the Gulf of Alaska may be limited by light, temperature, and other factors (Hobson 1980; McLain 1984). Although areas farther south may suffer from periodic El Nino/Southern Oscillation anomalies, their effects are less noticeable in the north where the "Aleutian Low" pressure system tends to dominate the cyclonic (counter-clockwise) atmospheric and oceanic patterns (Mysak 1986). Strong southeasterly currents and winds along the coast favor downwelling and onshore advection of warm plankton-laden surface waters from the Gulf of Alaska (Schumacher and Reed 1983; Cooney 1984). However, strength and location of the Aleutian Low appear to vary in concert with changes in other atmospheric systems, including the Southern Oscillation (Mysak 1986).

Anomalous sea surface temperatures, strengths of currents, sea level height, and salinities, all associated with unusual atmospheric events, are considered by many to be responsible for changes in marine biotic communities (e.g., Cushing 1975, 1981, 1982; Wooster 1983). Cycles in catch and average fish weight of sockeye salmon and recruitment of herring are coherent with 5-6 yr oscillations of physical factors in the Northeast Pacific, indicating that baroclinic waves in the ocean may affect fish populations (Mysak et al. 1982). Widespread synchrony in extreme year-class strengths of 59 stocks of marine fishes of the Northeast Pacific Ocean and significant pairwise correlations within (usually positive) and between (usually negative) region/species groups were attributed to the strong influence of environmental conditions on recruitment success (Hollowed et al. 1987). Recruitment of Southeast Alaska herring (*Clupea harengus pallasii*) has been correlated with temperature, salinity, sea level height, and moderate to strong El Nino episodes during the brood year (Pearcy 1983; Westpestad and Fried 1983; Mysak 1986). These observations are consistent with the hypothesis that

warm years may increase biological productivity in the Gulf of Alaska (McLain 1984).

Brights and other salmon stocks that rear in the Gulf of Alaska would presumably benefit from the increased productivity of warm years, but the same responses probably do not occur in more southerly areas where tules and other stocks rear. During El Nino years, such as 1958, there is a northward shift of currents and a reduction in the biomass density of zooplankton in the then-warmer waters off Vancouver Island (Mysak 1986). Survival of Columbia River hatchery stocks of tule fall chinook salmon, which rear in the area of Vancouver Island, has been negatively associated with temperature during their first marine year (Van Hynning 1973; Mathews 1984). Other contrasting responses of stocks in northern and southern areas of the North American Pacific Coast have been described (Pearcy 1983; McLain 1984; Peterman 1984; Hollowed et al. 1987).

It is quite clear that ocean conditions can affect the growth, and consequently the size and age at maturity, of Brights, but the magnitude and direction of the influence is less clear. Generalizations can be dangerous, because even two Columbia River fall chinook salmon stocks, Brights and tules, may respond oppositely to some of the same physical phenomena. Unfortunately, Brights have been studied only since the mid-1970s, and less than 10 complete cohorts have returned since that time. Rational speculation appears to be the only means of evaluating ocean effects on long-term changes in size and age at maturity of Brights. What can be deduced from the limited historical information available on ocean conditions in the Northeast Gulf of Alaska?

Changes in ocean conditions for growth probably did not contribute to the declines in size and age of Brights. Gulf of Alaska herring abundances had a highly significant negative correlation (using moving medians to describe long-term trend) with years for 1929-66 (extent of data series; Hollowed et al. 1987). Hence, the trend in abundance was downward during the period. This corresponds with a warming period up to the mid-1940s, then cooling until the 1970s in the Northeast Pacific Ocean (Ricker et al. 1978)

and worldwide (Cushing 1982). Strong year classes for Southeast Alaska herring during the 1957-58 El Nino were followed by weak year classes during the 1960s (Pearcy 1983). Assuming that low temperatures and herring abundances reflect low productivity and poor growth conditions for Brights, then a trend toward slower growth, later maturity, and larger mean size could be expected from the 1940s, or earlier, up through the 1960s. However, the opposite trend was actually observed for mean weight (Fig. 8). Ocean conditions probably were not responsible for the decline in mean weight in the run between the 1920s and 1950s and may well have opposed the real causes of the change.

Since the mid-1970s, however, conditions in the Gulf of Alaska have changed. There has been a weakening of the southeasterly trade winds, several years of anomalous northward transport of water, and high winter sea surface temperatures off British Columbia (McLain 1984; Royer 1984). Bristol Bay (Alaska) sockeye salmon, which also rear in the Gulf of Alaska, have shown improved growth associated with warmer winter temperatures during their marine lives (Eggers et al. 1984; Rogers 1984). Such occurrences, including the dramatic 1982-83 El Nino event, probably signal improved growth conditions and possibly earlier maturity for Brights. If so, then ocean conditions may have contributed to the low mean weights in the last decade. The conditions, however, would not likely be a major contributor to the decline, considering that the trend was contrary to expectations based on changes in ocean conditions in the earlier decades (1940s to mid-1970s).

Natural Mortality

Estimates of ocean mortality have been derived for chinook salmon (reviews by Ricker 1976; Healey and Heard 1984), but how those mortalities select for traits related to size and age at maturity is not well understood. Because it is a function of time, lifetime natural mortality is greater among the older-maturing fish, which may remain at sea 4-5 yr. Hence, an increase in natural mortality rate

could be expected to cause greater reductions in the older age classes and produce a lower mean age in the spawning population. There is no direct evidence that natural mortality rates have changed, but the trends in the ocean environment (e.g., declining productivity) between the mid-1940s and 1970s may have increased natural mortalities. If so, the expected reduction in older age classes due to higher mortality rates may have been offset by delayed maturity caused by slower growth. The net effect remains open to speculation.

Size-dependent survival is a fundamental premise of this paper and has been assumed for some models of marine natural mortality for Pacific salmon (e.g., Mathews and Buckley 1976). As in the early rearing environment, slow growth may cause prolonged exposure to size-selective agents of mortality during ocean life and disfavor those fish that would mature later. There is no conclusive evidence, however, that Brights are subject to size-selective ocean mortality, or that changes in selectivity of mortalities may have contributed to changes in mean age (hence size) of adults.

Unreported fishing-associated mortalities masquerade as natural mortality and may confound efforts to understand natural mortality processes. Changes in the rate and size-selectivity of fishing-associated mortality have the same potential effects on size and age at maturity as the changes in natural mortality mentioned above.

Ocean Fishing

Introduction As mentioned in previous sections, both immature and maturing Brights are probably taken by the northern fisheries off of Southeast Alaska, and the large numbers of Brights taken by British Columbia troll fisheries are probably maturing fish (Van Hying 1973; Funk 1981; Fraidenburg and Lincoln 1985; Howell et al. 1985a; PSC 1988). Low catches in the Washington coastal troll fisheries may be a result of the stock's late and rapid migration through the area (Utter et al. 1987). Since their origins early in this century, the Southeast Alaska and British Columbia ocean

fisheries have increased sufficiently in size and efficiency (Milne 1957; Fredin 1980) to possibly threaten the viability of Brights and other natural chinook salmon stocks taken in the fisheries (PST 1985; Fraidenburg and Lincoln 1985; Jensen 1986). How might these fisheries have contributed to the changes in Bright size and age?

Dr. Willis H. Rich (1925) was among the first of many fisheries scientists to condemn ocean fishing for its probably inevitable consequences of growth and recruitment overfishing. Cleaver (1969) and Henry (1971), respectively, estimated that ocean fishing caused 20% and 25% reductions in total yield (pounds) of some broods of Columbia River fall chinook salmon relative to a terminal harvest strategy. However, Ricker (1976) used the same data to estimate a 63-98% yield loss. Increased ocean fishing was identified as probably an important cause of declines in the Columbia River fall chinook salmon runs in the 1950s (Van Hyning 1973). Modelers have demonstrated how selectivity by ocean fisheries of certain life history types, such as those maturing at high ages, can lead to stock collapse (Hankin and Healey 1986; Hirai 1987).

Ocean fishing also has been identified as a potential cause of reduced size and age in Atlantic salmon (Paloheimo and Elson 1974; Schaffer and Elson 1975; Caswell et al. 1983; Bielak and Power 1986) and other stocks of chinook salmon (Ricker 1972, 1981; Henry 1971; Van Hyning 1973; Hankin and McKelvey 1985; Hankin and Healey 1986). Age selection occurs when some age classes, such as the youngest, are not as vulnerable to fishery-induced mortalities during a season and also when older-maturing fish are exploited for a greater number of seasons than those fish maturing earlier (see Nicholas and Hankin 1988, p. 173). Size selection occurs when size restrictions and/or fishing gears, areas, or times cause some sizes (often the largest) to bear higher mortality rates. Because of the close association between size and age, both types of selection can contribute to declines in size and age in a stock.

Ocean fishing may influence size and age in spawning populations in at least three nonexclusive ways. First, selection can cause relatively immediate size and age changes in escapements of

the cohorts subjected to the selection, and, second, it can also affect subsequent generations through changes in the stock genome. Third, whether selective or not, fishing also might reduce population densities to levels where compensatory growth is sufficient to decrease age at maturity (Miller 1956).

The purpose of this part of the study was to determine, if possible, whether the Southeast Alaska and British Columbia ocean fisheries are selective based on either size or age and whether the fisheries may have contributed to the decreases in size and age of Brights. The operable null hypothesis is that the fish taken in the ocean fisheries are similar in size and age as those that escape.

Methods Data for coded-wire-tagged Brights taken in fisheries and sampled in the escapement during recent years permit only rough comparisons of mean values for size, age, and size-at-age of known groups of fish. The appropriate standard for determining selectivity by a fishery is the differential (Appendix B) between measurements of a trait in the escaping spawning population with and without the fishery. However, no data are available from times when the fisheries did not exist, and the data that are available for escapement to the spawning areas are probably tainted by selection by intervening fisheries and other factors. Because of difficulties with expansions of CWT recoveries, I did not attempt to reconstruct the escaping run back through the preceding sequence of mortalities to the ocean fisheries. Unable to estimate a selection differential or even a difference between trait values in the catch and in the spawners escaping the fishery, I simply compared means of age and length-at-age for the landed catch of coded wire tagged Brights in a fishery with those returning to spawning areas in the Columbia River (escapement). Using age statistics avoids the effects of differences caused by within-season growth, but results can be influenced by differences in sampling effort among years and areas.

Mean ages were calculated from 1977-85 recovery data for Alaska and British Columbia commercial troll and net fisheries and for the two in-river fisheries (described in a later section) for each of six

CWT codes from Priest Rapids Hatchery for 1975-80 brood years (Appendix C). These means were then plotted against the escapement mean ages for the respective CWT codes.

Mean length at each age (3-5) and for each fishery for 14 Priest Rapids Hatchery CWT codes (1975-84 brood years, 1978-87 recoveries; Appendix C) were also compared with the escapement (data, including sample sizes, are in Appendix Table E.2). Recoveries of age 2 CWTs from the fisheries were negligible, and age 6 recoveries were rare in all areas, so those two age classes were not considered. Records with obviously erroneous length measurements were omitted. No statistical tests were applied. Sport fisheries and the Washington, Oregon, and California coastal commercial fisheries accounted for few recoveries and were not examined. Because in-river fisheries can affect the size and age composition of the escapement, the same data from those fisheries were also prepared for comparison.

Using raw numbers of tags recovered in the fisheries and escapement effectively assumes that relative levels of sampling effort between the two areas were consistent between years, otherwise changes in sampling intensity could distort the mean ages for tag code groups. Again, I did not attempt to determine sampling rates in the various years and recovery areas to expand the number of raw recoveries and account for any changes in sampling intensity.

Results Mean ages in both troll fisheries (Alaska and British Columbia) were uniformly higher than mean ages in the escapement, except for one tag code group for which mean age in the British Columbia troll fishery was essentially identical to that in the escapement (Fig. 23). Without exception, the mean age in the Southeast Alaska troll fishery was higher, by more than a year in one case, than the mean age for the same tag code group in the British Columbia troll fishery.

Minimum size limits are probably responsible for much of the differences in mean ages. The Southeast Alaska troll fishery, which may take many immatures in some areas, has had a 28 in. (71-cm, total length [TL], approximately 67 cm FL) minimum since 1978, although

from 1982 to 1984 it was legal to land fish of any size that had a clipped adipose fin (D. Mecum, Commer. Fish. Div., Alaska Dep. Fish Game, Juneau, AK, pers. comm. 6/90). The British Columbia troll fishery during this period was under a 62-cm FL minimum length restriction (PSC 1988), which probably permitted retention of more young fish. Most or all Brights harvested in the British Columbia troll fishery are probably maturing, but their higher ages (maturing fish would, on average, be older than immatures) may be insufficient to offset the more stringent selectivity imposed by the size limits in Southeast Alaska. Jacks and other small, early-maturing Brights may contribute proportionately more to the escapement because of minimum size limit protection in the ocean troll fisheries.

If the British Columbia troll fishery selects for large size (as it almost certainly does), then it can increase the apparent selectivity of the Southeast Alaska fishery by further depressing the mean age in the escaping spawners. Such is also the case with size selection in the in-river fisheries, which also appear to take generally larger (hence older) Brights (Fig. 23).

The net fisheries of Southeast Alaska and British Columbia show no consistent relationship to the escapement in terms of mean age (Fig. 23). The recoveries for CWT code groups in Southeast Alaska, which were relatively few (Appendix Table E.1), generally had higher mean ages than those in British Columbia net fisheries. Two very low mean ages (< 3 yr) for British Columbia suggest the presence of young, probably immature Brights in near-shore areas where the net fisheries occur, although mean ages for some other individual CWT code groups are higher than those in the escapement.

Patterns of mean size-at-age ratios differ among the types of fishery (Fig. 24). Among the CWT codes used for this comparison, the troll fisheries appear, overall, to take 3-yr-olds at sizes similar to those that escaped. The in-river fisheries also tended to take sizes of age 3 fish that were similar to the escapement and, therefore, probably had little effect on the ratios for the ocean fisheries.

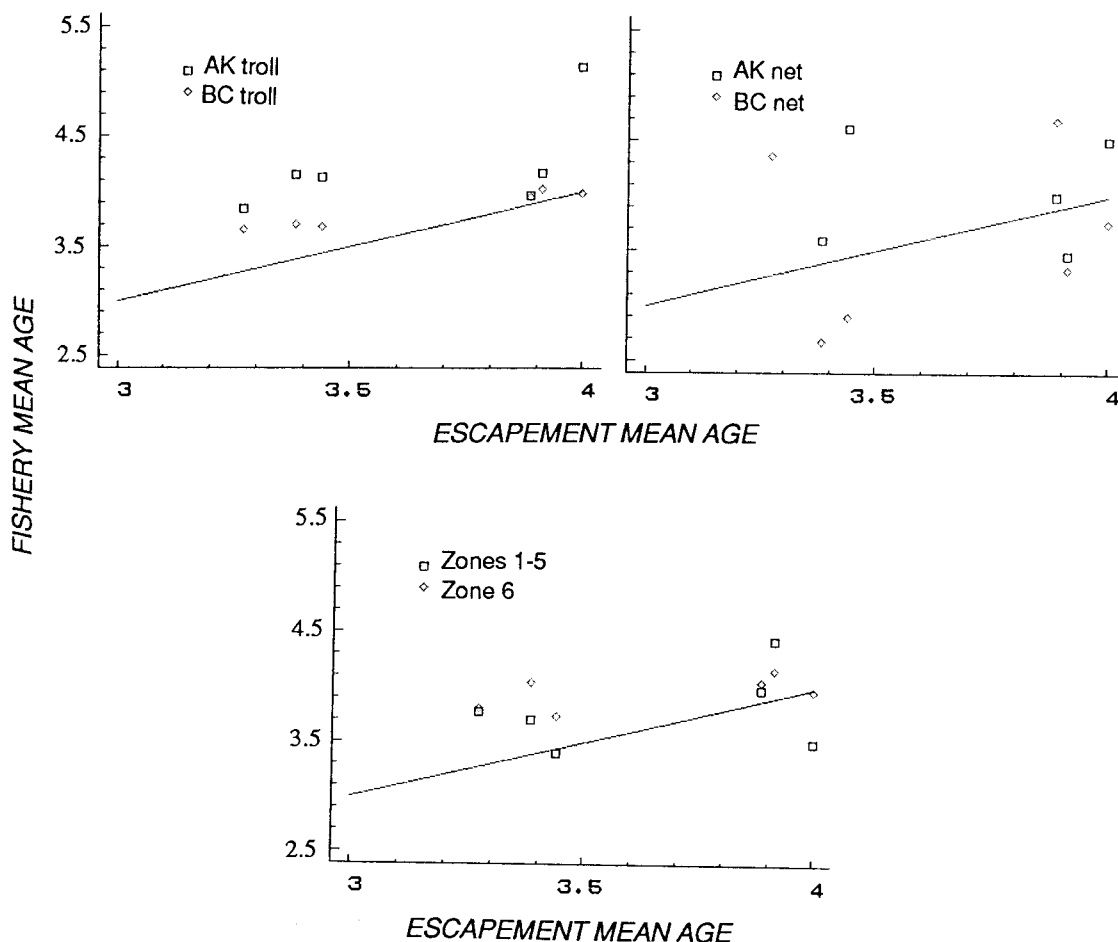


Figure 23. Mean ages of Brights taken in six ocean and in-river fisheries compared to mean ages in the escapement. Points represent six CWT code groups released from Priest Rapids Hatchery (data in Appendix Table E.1). The sloped line is identity; hence, a point above the line indicates mean age in the fishery is greater than in the escapement.

The mean sizes of 4- and 5-yr-olds in both troll fisheries are uniformly lower than the means for the same ages in the escapement (ratios < 1, Fig. 24). Lower mean sizes can be expected in fisheries that take immatures, which tend to be smaller than maturing fish at a given age (Ricker 1976), and also in fisheries occurring early in the growing season. In short, such a relationship may reflect harvesting before full growth is attained ("premature harvest"). It could also

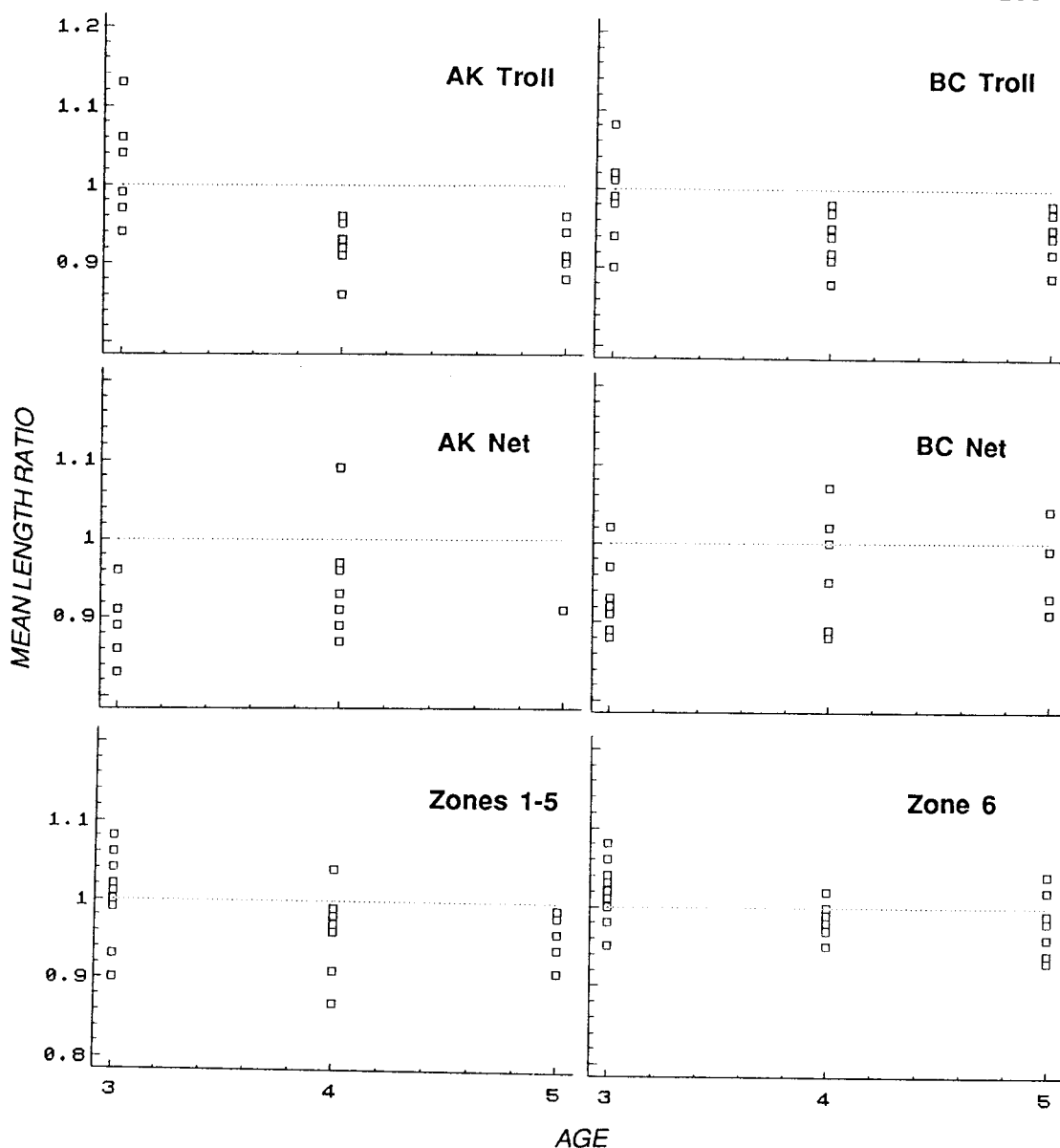


Figure 24. Comparison of mean length-at-age for Brights of several CWT code groups caught in ocean and in-river fisheries to mean length-at-age for the same groups sampled in the escapement. Each point at an age represents a different tag code group. Ratios are fishery mean length divided by escapement mean length; hence, ratios greater than unity (dotted lines) indicate fish taken by the fishery are larger at that particular age than those that escaped. Detailed data are in Appendix Tables E.2 and E.3.

mean that the largest fish are for some reason (e.g., different migrational behavior) less vulnerable to the fisheries. Premature harvest provides a plausible explanation for the low mean sizes in the Southeast Alaska fishery, where immatures are probably more common and maturing fish are probably harvested somewhat earlier in the season. However, premature harvest does not explain the very similar ratio distributions in British Columbia, where maturing fish that are approaching the end of their last marine season may prevail. (Recall the assertion that a large proportion of Brights taken in British Columbia fisheries, especially in those that occur offshore, are probably on their spawning migration to the Columbia River.) The in-river fisheries likewise took slightly smaller fish at ages 4 and 5, but it is unknown whether this selective removal depressed the ocean troll fisheries ratios by increasing mean sizes in the escapement.

The Southeast Alaska and British Columbia net fisheries present patterns of size at age that differ from those of the troll and in-river fisheries (Fig. 24). The low ratios at age 3 for both ocean net fisheries may reflect the absence of minimum size limits and/or the presence of smaller, immature fish in the catches. In the Southeast Alaska net fishery, mean sizes also were low relative to those in the escapement for ages 4 and 5. Means for the same ages in the British Columbia net fishery, however, were more similar to, but still less than those in the escapement. Such differences between the two areas would be expected if immature fish were more common in the inside net fisheries of Southeast Alaska and maturing fish of ages 4 and 5 were more common in the British Columbia net fishery areas.

Discussion These comparisons provide some evidence that the troll fisheries of Southeast Alaska and British Columbia are selective for size and age. Although Ricker (1981, p. 1638) stated that there "is no good information" regarding selectivity for large size by commercial troll fisheries, I believe that there is now sufficient evidence to merit some conclusions.

Ocean fisheries have probably contributed to the declines in size and age in Brights by causing increased mortalities of immature fish and by imposing higher mortalities on larger maturing fish, but the magnitude of the contribution remains unmeasurable. Immature Brights may be more prevalent in some areas of Southeast Alaska; hence, the increased retention and nonretention mortalities caused by development of troll and net fisheries in those areas would theoretically cause "juvenation of the age structure" in the stock (Ricker 1975, p. 260). Attempts to demonstrate this effect empirically, as through my comparisons, are obstructed not only by problems mentioned earlier, but by a lack of data on the maturity of fish in particular fishery areas and on the total mortality rates (as opposed to simply landed catch rates) imposed by the fisheries. Conclusions about the selectivity of ocean fisheries must still be somewhat tentative, for they are founded as much on knowledge and assumptions about how the fisheries operate as on direct and unequivocal evidence.

Minimum size limits in troll fisheries, often employed to reduce harvests of immature fish, can contribute to the nonretention component of total fishing-induced mortalities of immatures and to direct size selection of the maturing fish. Although immediate and short-term hooking mortality of released sublegal-size (< 71 cm TL, approximately 67 cm FL) chinook salmon may be as low as 25-26% (Wertheimer 1988; Wertheimer et al. 1989), other estimates have generally been higher (review by Ricker 1976). These nonretention mortalities prompted Funk (1981) to recommend management of troll fisheries in Southeast Alaska by time and area, rather than minimum size restrictions, to maximize yield. Among maturing fish, which those Brights taken in the British Columbia troll fishery probably are, minimum size limits increase the average size of the landed fish, decrease the average size in the escapement, and cause some nonretention mortalities. Increases in the minimum size limit, without a balancing reduction in the number of fish landed, heightens these effects (unpublished MS available from the author).

Nonretention mortalities have become a concern for monitoring the effectiveness of catch quota ceilings imposed under the US-Canada Pacific Salmon Treaty (PST). The minimum size limit in the British Columbia commercial troll fishery in outside waters was increased from 62 cm to 67 cm FL in 1987 (PSC 1988); a similar increase was made in Southeast Alaska several years earlier (D. Mecum, Commer. Fish. Div., Alaska Dep. Fish Game, Juneau, AK, pers. comm. 6/90). Because the catch quota ceilings are based on numbers of fish landed and value of the catch is based on weight landed, the increase in the minimum size limit causes "high-grading" of the catch: only the largest and most valuable fish caught are retained and counted against the quota. In Southeast Alaska, some fisheries targeting on other species (e.g., trolling for coho salmon, purse seining for pink salmon) catch chinook salmon, but are not allowed to retain them during some periods (ADFG and NMFS 1987). Mortalities among nonretained chinook salmon in some fisheries are believed to be high (e.g., 50-90% in purse seine fisheries, 20-30% in troll fisheries; ADFG and NMFS 1987). Chinook salmon nonretention regulations appear to be attempts at double-standard accounting, a way of permitting fishing-induced mortalities while creating the illusion that conservation measures (such as catch quota ceilings) are being upheld. However, efforts to monitor the effectiveness of implementation of the PST conservation measures now incorporate adjustments for fishing-induced mortalities, and there apparently has been little or no reduction, between the 1979-82 base period and 1987, in the rates at which Southeast Alaska and British Columbia ocean fisheries exploit Brights and other chinook salmon stocks (PSC 1988).

Fishing-induced mortalities, and harvest regulations that encourage them, are of interest to this study for three primary reasons. One, data from the landed catch, as used in this study, provide an incomplete record of potential fishery impacts on the size and age structure of a stock. Two, increases in the proportion of nonretention mortalities may have a substantial influence on the size and age of Brights. Nonretention mortalities among immature fish

disfavor those that mature at older ages, acting as would an increment to the annual natural mortality rate. An increase in the minimum size limit increases the number of sublegal size fish that incur hooking mortalities (although decreasing the total fishing mortality on this group), but concentrates full fishing and retention mortalities on the larger, later-maturing life history types in a stock. Three, conservation and management measures expressed simply in terms of numbers of fish are inadequate; they do not address some fundamental measures of resource value (e.g., weight of fish caught, fecundity of the escapement). For example, retention of only the largest fish taken by a fishery can increase the value of the catch (landed weight plus a premium for large fish)⁴ and reduce the reproductive potential of the escapement (e.g., number surviving, percent females, eggs per female), even with a reduction in the number landed. Such a scenario is clearly contrary to the intentions of the PST and prudent resource management (Funk 1981). Greater attention to measures such as size and/or age of the fish, in addition to numbers, could improve management effectiveness if it led to promulgation of more appropriate regulations. (See further discussion in Harvest Management, p. 167.)

If it could be proved that the ocean fisheries have contributed to the decline in mean size of spawning Brights, the question of consequences must still be answered (Larkin 1981). In the introduction to this section I listed three nonexclusive ways that the effects of ocean fishing could influence the size and age in the spawning escapement. Ricker (1980, 1981) argues that selection by ocean fisheries probably has been an agent of changes in the genetic bases of size and age in chinook salmon stocks (my second influence) and that such changes are particularly serious because they are largely irreversible. Others, however, point out that (1) fisheries account for only a small fraction of the total lifetime mortalities, (2) fisheries may not be directionally selective in a strong and

⁴ E. Critchlow, Portland Fish Wholesale Co., Portland, OR, pers. comm. 6/90; D. Gaudet, Commer. Fish Div., Alaska Dep. Fish Game, Juneau, AK, pers. comm. 6/90.

consistent manner, (3) other selective factors could counteract the selection by fisheries, and (4) the demographic response to reduced densities (my third influence) is phenotypically identical to the genetic response to size and age selection predicted by life history theory (Healey 1986; Porter et al. 1986; Riddell 1986).

The lack of unambiguous evidence that fisheries change the genetic bases for size and age at maturity should be considered a result of problems with detection and not necessarily a lack of occurrence (Nelson and Soule 1987). The high apparent heritability of size and age at maturity, the known and probable selection on these traits by ocean fisheries, and the demonstrated change in size and age of Brights and other salmon stocks suggest at least a partial cause and effect relationship. The consequences of the size and age declines (the subject of a later chapter) and the relative immutability of genetic changes for these traits recommend that ocean fisheries be managed conservatively to preserve the larger and older life history types in salmon stocks.

Ocean Summary

Growth conditions for Brights are probably dependent on large-scale climatic and oceanographic processes that govern production in the Northeast Gulf of Alaska. Trends in ocean temperature and abundance of important forage fishes suggest that conditions from the mid-1940s to mid-1970s may have been less favorable for growth of Brights than during earlier and more recent periods. The decreasing size of Brights during the period of poor conditions is not consistent with the hypothesis that slower growth tends to delay maturity and cause an overall larger mean size in the escapement. Hence, I conclude that ocean growth conditions probably were not very influential in the declines in mean size and age of Brights.

An increase in natural mortality rates would, theoretically, favor those fish maturing earlier (at small size). However, extremely little is known about what these rates are for Brights and

how changes in them may have contributed to a change in size at maturity.

The ocean fisheries of Southeast Alaska and British Columbia appear to select against large size and older age in the spawning escapement of Brights. Such a conclusion is based as much on knowledge and assumptions regarding the operation of the fisheries (e.g., minimum size limits, presence of immature Brights, unreported mortalities) as on analysis of size and age data taken from coded wire tagged Brights in the catch and escapement. It is not known whether the selection (if any) in these fisheries has intensified over the period in which the decline in size occurred. The exact nature of potential size and age changes resulting from ocean fishing is still being debated.

Ocean fishing is inconsistent with maximum yield and conservation objectives. This assertion is supported by recent ocean harvest tactics that create the illusion of compliance with PST-mandated reductions in exploitation rates. Such tactics also underscore the need for management objectives and regulations based on more realistic measures of resource value (e.g., biomass landed, adult equivalents killed, egg potential in the escapement) than simply numbers of fish landed and escaped.

Spawning Migration

When the necessary physical and physiological conditions are satisfied, Brights begin to mature and commence their spawning migration. The journey up the Columbia River has probably always been challenging. Migrational barriers and, in recent millennia (particularly the last 130 yr), fisheries of increasing intensity have reduced and probably shaped the characteristics of the spawning population. The objective of this portion of the study was to explore the in-river fisheries and migrational obstacles to understand whether and how they may have contributed to declines in size of Brights.

In-river Fisheries

Introduction The Columbia River salmon fisheries were once a rich (albeit overly developed) blend of devices, personalities, and enterprises (Craig and Hacker 1940). In the fight for continued access to the diminishing resource, dominant gillnetters politically eliminated competing gear groups (except dipnetters) by 1950 (Wendler 1966, Smith 1979). The filling of the reservoir (Lake Celilo) behind The Dalles Dam in 1957 extinguished the predominantly Indian dipnet fishery at Celilo Falls (Fig. 25) (Cramer 1974), and commercial fishing above Bonneville Dam was banned in the same year (Wendler 1966). The Indian fishery resurrected itself as a set-gillnet fishery in the Bonneville pool (reservoir), and by 1964 was harvesting approximately as many salmon as did the Celilo Falls dipnet fishery during its final year (Maltzeff 1965). Commercial fishing in Zone 6, the management area between Bonneville and McNary dams, has been restricted to treaty Indian fishers since 1969 (Young and Robinson 1974). Various circumstances have resulted in the commercial fisheries in the Columbia River using gillnets, probably the most size-selective gear ever deployed on the river (a minor amount of dipnetting still occurs in Zone 6, however).

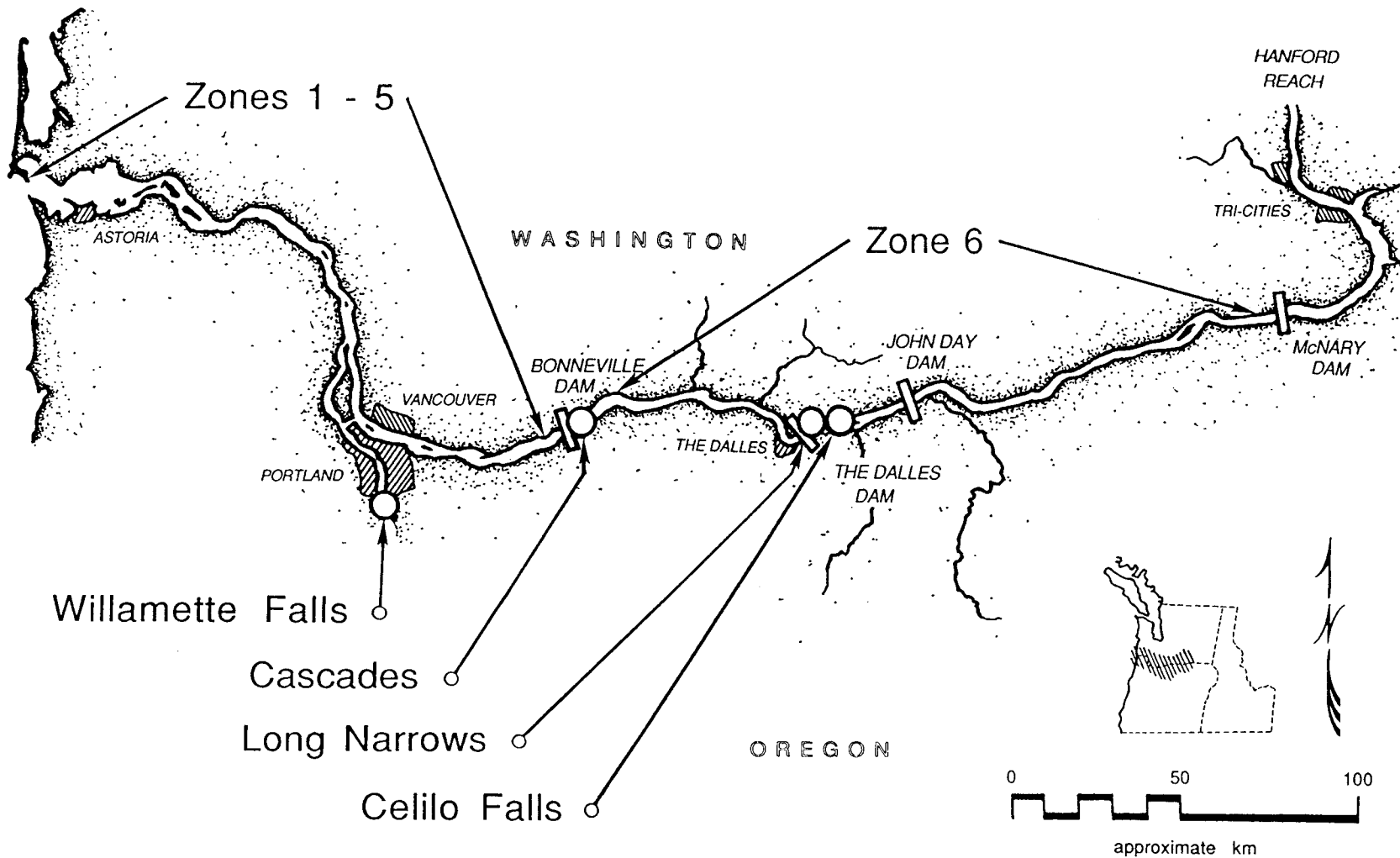


Figure 25. Locations of present-day in-river commercial salmon fisheries and former hydraulic features that may have been barriers to upstream migration of anadromous salmonids.

Harvests of Columbia River fall chinook salmon are allocated (numbers of fish) among ocean and in-river fisheries through negotiations involving a host of management agencies, tribal representatives, and other users (Madson and Koss 1988). The PST and decisions regarding Indian treaty entitlements by the U.S. 9th Circuit Court (see *United States v. Oregon* in CRITFC 1987) provide the major legal framework for allocation decisions. The Technical Advisory Committee, comprising representatives of fishery agencies and tribes involved with *United States v. Oregon*, formulates in-season management recommendations (e.g., gear and season restrictions) for adoption by the regulatory bodies of the tribes and states. Regulatory consistency within Zones 1-5 is maintained through the Columbia River Compact between Oregon and Washington (Wendler 1966) and within Zone 6 through participation by the four treaty tribes in the Columbia River Inter-Tribal Fish Commission.

Like the fall chinook salmon stocks, the in-river fall commercial fishing seasons have diminished. During the first half of this century, fishing (open seasons) for fall chinook salmon was uninterrupted except for the traditional late-August to 10 September closure (Wendler 1966). Fishery managers now attempt to distribute effort throughout the course of the run, but are often constrained by the presence and vulnerability of depressed stocks (e.g., summer-run steelhead early in the fall run). Protecting the steelhead from incidental harvest has also been the primary rationale for minimum gillnet mesh size restrictions during some early fall fishing seasons since at least 1969 (FCO and WDF 1971-72, ODFW and WDF 1977-85).

Recreational harvests were not examined because they have taken few Brights relative to the commercial fisheries (ODFW and WDF 1988). Likewise, the ceremonial and subsistence catches by the treaty tribes were not considered.

The working premise for this part of the study was that the in-river fisheries are, and have been, selective for size of Brights in ways that could have contributed to the observed decline. Of particular interest were potential differences in run timing related to fish size and in size selectivity of the gears deployed in the

commercial gillnet fisheries. The null hypotheses were: 1) there is no difference in run timing of Brights based on fish size; 2) if there is temporal separation by size, then the effort by the fisheries is evenly distributed throughout the run; 3) gear (gillnet mesh size) restrictions have no effect on the size of fish caught; and 4) there is no difference between the size of Brights taken in the fisheries and those recovered in the spawning areas. Comparisons focused on size rather than age of fish.

Methods Size selection can occur if the different sizes of fish tend to migrate through the fisheries at different times and if fishing effort tends to be differentially applied during the run. Counts of chinook salmon passing The Dalles Dam after 1 August (although the fall run officially begins on 4 August at The Dalles) were examined for differences in mean date of passage for jacks (for 1962-87) and adults (for 1960-87). Jacks are here defined by size, with 18 in. (45.7 cm) used as the upper length limit for jacks prior to 1964 and 22 in (55.9 cm) used since (USACE 1963, 1964). In the analysis, jacks represented small Brights and adults represented larger fish. Because Brights compose the majority of fall chinook salmon production above The Dalles Dam, I assumed that the fall chinook salmon counted there are almost exclusively Brights, with the exception of a few stray and transplanted tule fall chinook salmon.

The annual mean dates of passage for jacks and adults at The Dalles Dam (provided by B. P. Lumley from the CRITFC dam count database) were examined for consistent differences using Wilcoxon's signed-ranks test (Sokal and Rohlf 1981). Student's *t* (for slope of regression line) and the nonparametric Cox-Stuart test (Daniel 1990) were used to test trends within and between the two sets (i.e., for jacks and adults) of mean passage dates.

No method was found to measure the relative intensity of fishing effort applied to Brights during the various portions of the run. It may take individual Brights 1-2 wk to transit each of the two fishery areas, Zones 1-5 and Zone 6, which span approximately 225 and 209 km (140 and 130 river mi), respectively (ODFW and WDF 1988).

Hence, catches reported within an area may include both early-running fish taken in the upper portion of the fishery and late-running fish just entering the lower portion of the fishery. Gear restrictions that create size selection and periods when nets of potentially different effectiveness may be used further confound an interpretation of within-year distribution of effort.

The size selectivity of the fisheries was somewhat easier to measure. Two general comparisons were made: (1) between fish caught under an 8-in minimum mesh-size restriction and those taken when mesh size was unrestricted (gear comparison), and (2) between fish caught in the fishery and those found in the escapement to spawning areas (fishery comparison). Although an assortment of gillnet mesh-size restrictions has been applied during fall seasons in the two areas, an 8-in minimum has been by far the most common in recent years. I hypothesized that the 8-in minimum restriction would force fishers to use gillnets with larger mesh sizes than would otherwise be deployed and hence catch larger fish.

For the gear comparison I matched recoveries of CWTs bearing Priest Rapids Hatchery codes (Appendix C) in the two fishery areas during 1978-87 (provided by C. Corrarino, ODFW, Portland, OR) with the mesh restrictions in effect during the time and in the area of capture (ODFW and WDF 1978-88). Individual recoveries for all codes were aggregated to provide a single sample of fish lengths for each year, area, and gear restriction (several broods and ages, represented by different codes, would be present each year). Hence I assumed that the same assortment and proportions of codes were equally available for capture during the periods when the two mesh restrictions were in effect. In other words, I assumed that the mix of codes that was present during the unrestricted seasons was also present during the 8-in minimum seasons in the same year and fishery. I know of no method for testing this assumption; the only samples taken from the populations in the river were by the fisheries that are being examined. Separate comparisons were also made for each sex.

Similarly, recoveries of CWT codes applied to outmigrating 1980-82 brood subyearling chinook salmon at McNary Dam during National Marine Fisheries Service (NMFS) studies (Appendix C) were also aggregated by year, area, gear restriction, and sex for similar comparisons on an alternative group. Subyearlings in the NMFS studies at McNary were probably primarily Brights from the Hanford Reach, although some individuals from other Columbia River and Snake River summer and fall chinook salmon stocks were no doubt included.

Adequate recoveries to provide meaningful comparisons between the two mesh size regimes (unrestricted and 8-in minimum) were obtained in Zone 6 during 1985 and 1986 and in Zones 1-5 in 1987. Both CWT code groups (i.e., PRH and NMFS) were adequately represented in the Zone 6 data in 1985 and 1986, but only the Priest Rapids Hatchery CWT code group was well represented in the Zones 1-5 data in 1987. Therefore, five comparisons were possible for each sex.

The Mann-Whitney *U* statistic (STSC, Inc. 1987) was used to test the differences in mean lengths between the two mesh regimes within each year, CWT code group, and area stratum for the two sexes. The sex compositions of the two regimes were compared (chi-square statistic with Yates' correction; Sokal and Rohlf 1981) within the strata to illuminate any sex selection potentially accompanying size selection. (Because they generally mature at older ages, female Brights have higher average size than males.) The Wilcoxon two sample (signed ranks) test (Sokal and Rohlf 1981; STSC, Inc. 1987) was used to compare mean size (by sex) and sex composition across years and tag code groups to determine if either regime consistently took larger fish or more females.

A parallel set of comparisons was made with jacks (here identified as 2-yr-olds, all males) omitted from the data. Some fishery managers assume that jacks, because of their small size, are so competitively inferior to adult males on the spawning ground that they make a negligible contribution to the next generation (M. Matylewich, CRITFC, pers. comm. 5/89). Whether jack Brights have negligible fitness is not known, but the possibility raises questions about their inclusion or exclusion in any study of size selection and

heritability in a natural population. This parallel comparison demonstrates what the selective impacts are on the spawning Bright stock if jacks do indeed lack the ability to reproduce under prevailing natural conditions.

The second general comparison, between the overall catch in the fisheries and the escapement (fishery comparison), employed methods similar to those used for the gear comparison. However, only Priest Rapids Hatchery CWT codes were used (Appendix C). Within each return year, recoveries were aggregated by area (i.e., escapement, Zones 1-5, and Zone 6) and sex. Sexes were also combined for one analysis to examine overall effects. Recoveries of the codes from Priest Rapids Hatchery volunteer and conscript spawners and from carcasses sampled during spawning ground surveys in the Hanford Reach and between Priest Rapids and Wanapum dams represented the escapement (data from S. Markey, WDF, Olympia, WA). For 1985-87, when numerous recoveries were made under each of two different gear regimes (i.e., unrestricted or 8-in minimum mesh size) in a fishery, those recoveries were aggregated separately and compared to the escapement. For all other years, 1978-84, no distinction was made based on gear restrictions. Mean lengths in the fisheries were compared to those in the escapement for each year and gear (i.e., mesh size) stratum with the Mann-Whitney *U* statistic (STSC, Inc. 1987) for the two sexes. Within-year differences in sex composition between fisheries and escapement were tested with the chi-square statistic. Overall differences in mean lengths and sex composition between fisheries and the escapement across years (1978-87) were evaluated with the Wilcoxon signed ranks test (STSC, Inc. 1987). Two parallel analyses were also made for the fishery comparison, one with jacks excluded (ages 3-6, only) and the other with the two sexes combined.

The Bright runs from 1984 to 1987 were reconstructed from the escapement back through the two in-river commercial fisheries and selection differentials (Appendix B) for size were estimated. The reconstruction used estimates of adults (ages ≥ 3 yr) harvested commercially and escaped for the entire upriver bright stock complex (ODFW and WDF 1988, Table 27), but did not include the sport catch.

The mean lengths of the fish coded wire tagged at Priest Rapids Hatchery (both sexes combined) sampled in the fisheries and the escapement were used to represent all of the Brights harvested and escaped, although the Priest Rapids Hatchery fish probably do not accurately represent the entire run (see following Discussion). Prior to 1984, too few coded wire tagged fish from Priest Rapids Hatchery were recovered in some areas during some years for the mean length samples to be considered even remotely representative of the run.

Again, estimates were computed both for all ages and for adults (ages ≥ 3) only. Because the estimated numbers available for caught and escaped fish were for adults only, those numbers were adjusted for the all-ages estimates by expanding by the factor $1/(1-P_j)$, where P_j is the proportion of jacks in the sample from a particular fishery or escapement and year. For example, if an estimated 50,000 adults were taken in Zones 1-5 in a particular year and samples from the fishery showed that 0.05 of the catch was jacks, the adjusted estimate of the number taken (all ages) is $50,000/0.95 = 52,632$. The relevant mean lengths (adults only or all ages) were weighted by the estimated numbers (adults) or adjusted estimated numbers (all ages) of fish in the escapement or removed by a fishery to determine the approximate mean lengths of fish entering and escaping the fisheries.

Results Counts of jack and adult fall chinook at The Dalles Dam show a changing relationship in mean dates when the two groups passed The Dalles Dam (Fig. 26). In the 26 yr from 1962 to 1987, the mean date of passage became significantly later for jacks (16 d; Cox-Stuart $Z = 3.33$, $P < 0.001$), but not significantly later for adults (4 d; Cox-Stuart $Z = 1.44$, $P = 0.15$). Based on the trends for the two groups, jacks passed The Dalles Dam earlier than adults before 1971 (Wilcoxon signed-ranks, $Z = 2.37$, $P < 0.02$), but later than adults after 1971 (Wilcoxon signed-ranks, $Z = 3.02$, $P < 0.01$). By 1987, the mean passage date of jacks followed that of adults by

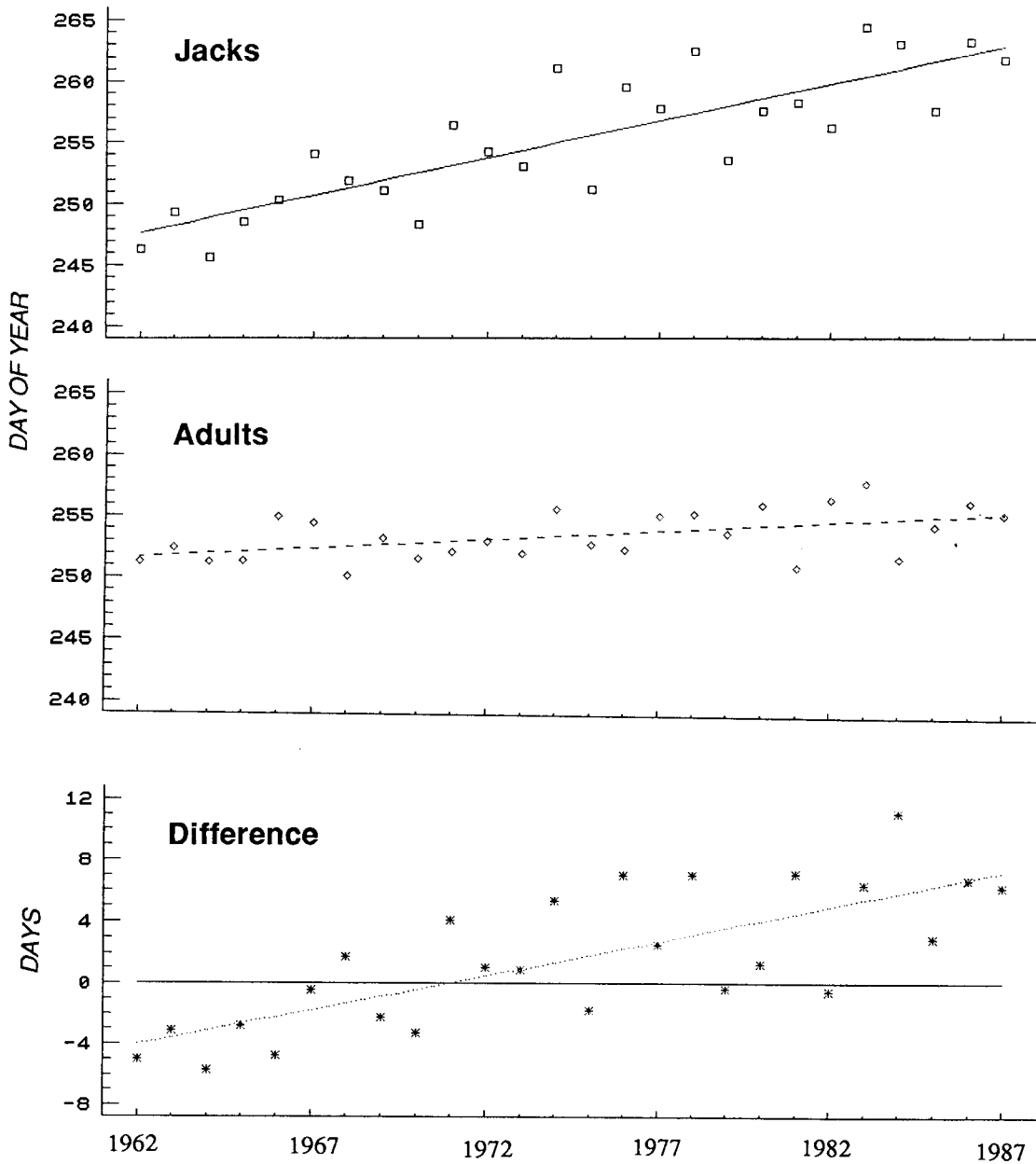


Figure 26. Mean day of passage for jack and adult fall chinook salmon (primarily Brights) at The Dalles Dam, 1962-87. "Difference" is mean day of adult passage minus mean day of jack passage. Day 244 is 1 September, except in leap years. Trend lines are from least-squares regression:

	<u>slope (P)</u>	<u>intercept</u>	<u>r²</u>
Jacks	0.61 (<0.001)	210.1	0.71
Adults	0.16 (0.15)	241.8	0.33
Difference	0.45 (<0.02)	-31.8	0.57

Detailed data are in Appendix H.

approximately 1 wk. The mean date of passage for jacks moved later at a significantly greater rate than that of adults during the period (Fig. 26; Cox-Stuart test on difference in annual mean dates, $Z = 3.33$, $P < 0.001$).

Assuming that the migration timing of jacks represents the extreme case for small fish (jacks are the smallest members of the spawning run), then smaller fish were probably relatively more abundant early in the run between 1962 and 1971 (timing prior to 1962 is not known), but later in the run after 1971. This demonstrates the potential for size selection if fishing effort tends to be differentially applied to the earlier or later portion of the run, but I was unable to obtain data that would accurately describe the application of effort relative to the mode of the Bright run. Hence, I could not determine if larger and smaller Brights are likely to have been differentially harvested based on timing of effort during the run.

In general, the gear comparison did not show that the 8-in. minimum mesh size restrictions resulted in the capture of consistently larger fish (Fig. 27). The average size of males taken under the 8-in minimum regime was generally greater than those taken under the unrestricted regime, but the differences were statistically significant ($P \leq 0.05$) in only one case (1985, PRH code group, Zone 6) (Appendix Tables F.4 and F.5). This was true regardless of whether jacks were included (all ages) or excluded (ages 3-6).

For females the results were less consistent (Fig. 27). The only statistically significant ($P \leq 0.05$) difference was the 1987 comparison in Zones 1-5 in which the average female size was substantially larger under the 8-in minimum regime. The same comparison for males yielded a similar, although not statistically significant, difference. The size of females caught appears to be more closely associated with the gear restrictions applied to Zones 1-5 in 1987 than to Zone 6 in 1985 and 1986. Excluding jacks had no effect on the comparisons for females.

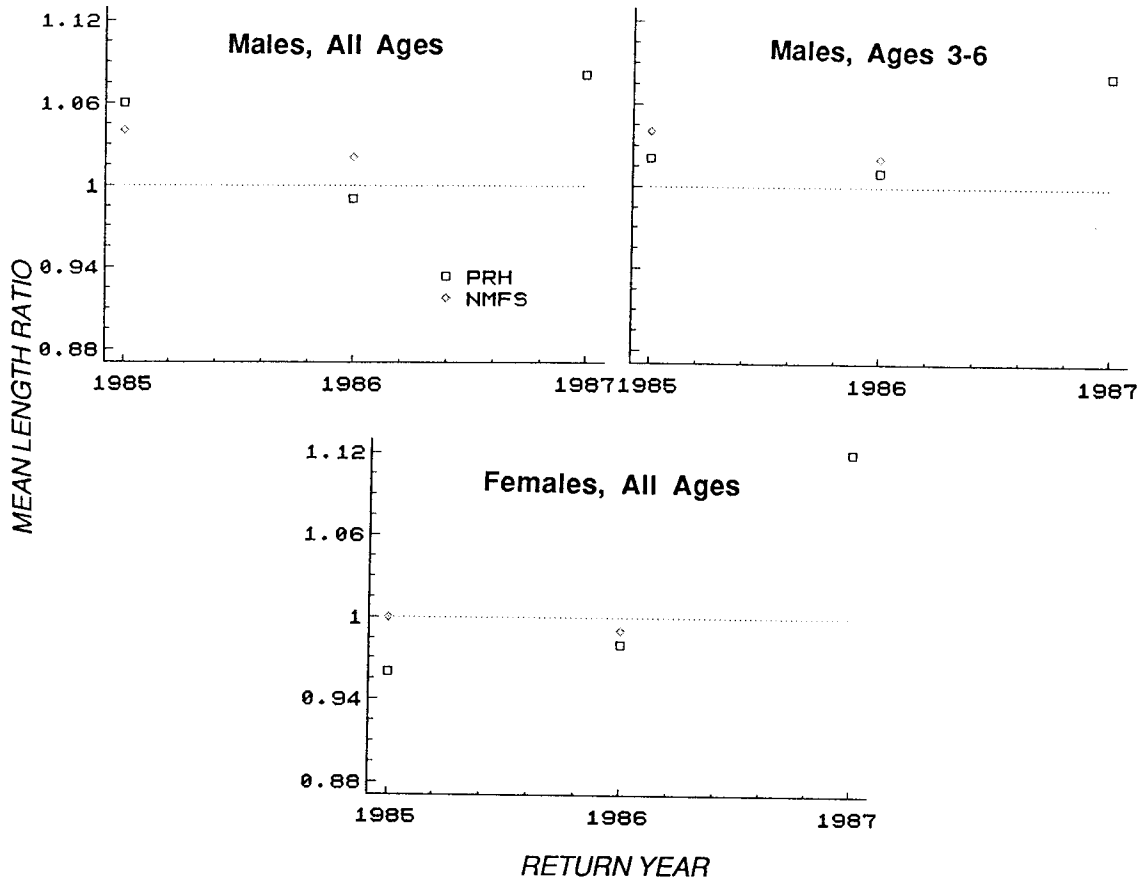


Figure 27. Comparison of mean lengths of Brights taken in the Zone 1-5 (1987) and Zone 6 (1985 and 1986) commercial gillnet fisheries under 8-in minimum and unrestricted mesh size regulations during the same year. Ratios are mean lengths under the 8-in minimum restriction divided by mean length when mesh size was unrestricted; hence, values greater than unity (dotted line) indicate larger fish were taken under the 8-in minimum restriction. PRH=Brights tagged and released at Priest Rapids Hatchery; NMFS=Brights collected as juveniles at McNary Dam during studies by NMFS. See Appendix Tables F.4 and F.5 for data.

The sex composition of the catches under the two regimes did not differ significantly in any of the five comparisons (Appendix Tables F.4 and F.5).

In the years examined, the two in-river fisheries took larger males, took smaller females, and overall tended to take larger fish than were found in the escapement. When both sexes and all ages were combined, larger fish were taken in the fisheries than were sampled in the escapement (Table 2). In 11 of the 13 comparisons (for both fisheries) that yielded statistically significant ($P \leq 0.05$) differences, the mean length of the catch was greater than the mean length of the escapement. For males (all ages), all 13 significant differences in mean length resulted from the fisheries taking larger fish. Conversely, 13 of the 14 significant differences for females (all ages) resulted from the fisheries taking smaller fish of that sex. That the fisheries can have opposing effects on the two sexes with regard to size selection is particularly apparent in the 1986 comparison of the Zone 6 catch (under an 8-in minimum restriction) to the escapement (Fig. 28). The opposing directions for selection of the two sexes appears to be the result of sexual dimorphism in size; males (particularly jacks) generally mature at an earlier age (hence smaller size) than females. Excluding jacks did not substantially change the results of the analyses (Table 2).

The selection differentials estimated by reconstructing the runs in 1984-87 also show that the in-river fisheries probably depressed the size of fish in the spawning runs during those years (Table 3). The Zone 6 fishery appears to have had the greater impact (all ages), and the overall differential caused by both fisheries was estimated to be as high as 45 mm (1986). If accurate, this indicates that in 1986 the mean size in the escapement was 45 mm less than the mean size of the run entering the river due to removals of larger fish by the commercial fisheries. For adults only, the differentials are less negative and, overall, not consistent with respect to the direction of change presumably caused by the fisheries.

The fisheries took not only larger fish than were found in the escapement, but also tended to take higher proportions of females

Table 2. Summary of results of Mann-Whitney *U* tests between lengths in catches by in-river fisheries and lengths in the escapement of Brights coded wire tagged as juveniles at Priest Rapids Hatchery. For "Fishery": Z1-5 = Zones 1-5; Z6 = Zone 6. *n* = number of year/gear strata compared. ** = significant at $P \leq 0.01$; * = significant at $P \leq 0.05$; ns = not significant. See Appendix F for detailed results.

Sex/ Ages	Fishery	<i>n</i>	Fishery Length < Escapement				Fishery Length > Escapement			
			**	*	ns	Equal	ns	*	**	
Both/ All	Z1-5	11	0	2	0	0	5	1	3	
	Z6	12	0	0	2	0	3	0	7	
Male/ All	Z1-5	9	0	0	2	0	2	2	3	
	Z6	12	0	0	1	0	3	2	6	
Female/ All	Z1-5	11	5	2	3	0	0	1	0	
	Z6	12	5	1	4	0	2	0	0	
Male/ 3-6	Z1-5	9	1	0	2	1	3	0	2	
	Z6	12	0	0	3	0	3	1	5	

(Table 4). This was true even when the comparisons were restricted to adults (ages 3-6, only). All significant differences in sex composition of the catch and escapement occurred when the fisheries took higher proportions of females than were found in the escapement.

Discussion The run timing of small (jack) Brights passing The Dalles Dam has become later since 1962. The mean date of passage for adults may be retreating as well, but at a significantly slower rate than that for jacks. The later migration of small Brights is consistent with the downward trend in mean size of females observed during the course of the spawning season, as discussed earlier.

Size-related differences in run timing are common. For example, Van Hying (1973) states that it is "well known" that males (BPH tule fall chinook salmon) precede females in arrival at the hatchery, particularly jacks. Earlier timing of jacks in Oregon

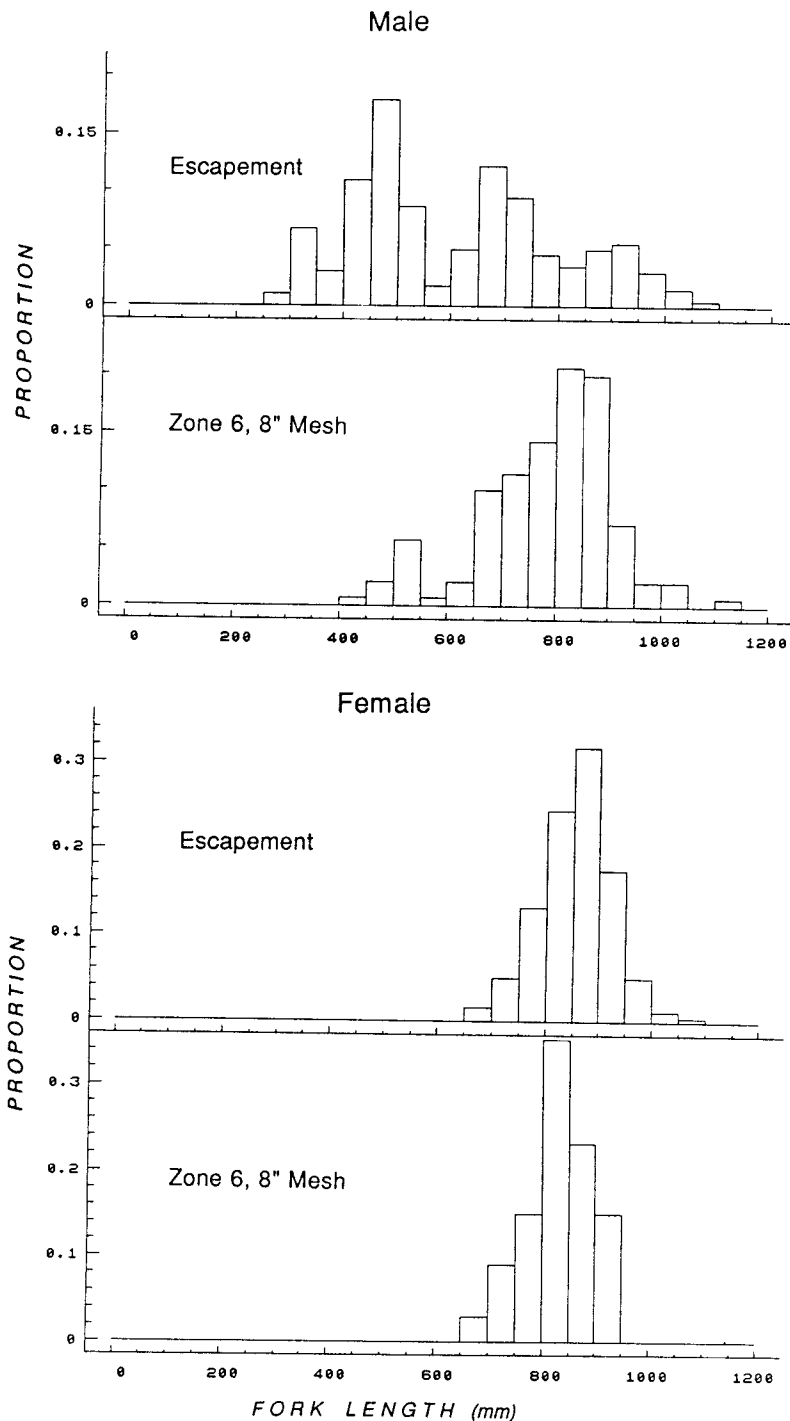


Figure 28. Apparent selection by the Zone 6 fishery of large male and small female Brights. Length distributions of coded wire tagged Brights taken under an 8-in minimum mesh size restriction in the fishery compared to recoveries from the spawning ground and Priest Rapids Hatchery in 1986. Length differences between catch and escapement are highly significant ($P < 0.01$) for both sexes (see Appendix Table F.2).

Table 3. Selection differentials for length in the in-river fisheries. Computations assume that the lengths of all Brights are represented by fish coded wire tagged at Priest Rapids Hatchery. See Appendix G for detailed information.

Year	Selection Differentials (mm)		
	Zones 1-5	Zone 6	Both Fisheries
	<u>All Ages</u>		
1984	8	- 6	2
1985	- 3	-19	-23
1986	- 8	-37	-45
1987	-13	-26	-39
	<u>Adults Only</u>		
1984	19	7	26
1985	4	- 2	1
1986	6	- 1	5
1987	-12	-26	-38

Table 4. Summary of results of chi-square contingency tests between sex compositions in catches by in-river fisheries and those in the escapement of Brights coded wire tagged as juveniles at Priest Rapids Hatchery. For "Fishery": Z1-5 = Zones 1-5; Z6 = Zone 6. n = number of year/gear strata compared; ** = significant at $P \leq 0.01$; * = significant at $P \leq 0.05$; ns = not significant. Strata with inadequate sample sizes for testing are not included. See Appendix F for detailed results.

Ages	Fishery	n	Fishery % Female <u>< Escapement</u>			Fishery % Female <u>> Escapement</u>		
			**	*	ns	ns	*	**
All	Z1-5	9	0	0	0	4	1	4
	Z6	12	0	0	0	5	0	7
	Both	21	0	0	0	9	1	11
3-6	Z1-5	8	0	0	2	3	1	2
	Z6	11	0	0	3	4	2	2
	Both	19	0	0	5	7	3	4

coastal stocks of fall chinook salmon may be associated with differential stream passability (based on fish size) during seasonally variable flows (Nicholas and Hankin 1988). The apparently later arrival (relative to adults) of jack Brights at Rock Island Dam on the middle Columbia River since 1963 (Mullan 1987) probably resulted in large part from major removals of adults downstream at Priest Rapids Dam for hatchery brood stock (Allen and Meekin 1973; subsequent section of this paper). Data from The Dalles Dam indicate that jack Brights passed earlier than adults until about 1971, when a trend toward later migration caused them to pass later than the larger adults. Apparent differences in timing of the two size groups of Brights may reflect to some degree differences in abundance, timing, and/or average fish sizes of Bright substocks. The trends and changes in size-related run timing for Brights indicate not only that general rules of thumb about size-related run timing are tenuous, but that fisheries on Brights are not likely to have been consistently size-selective based on when during the season effort was applied. I was unable to derive any measure of effort relative to run timing that could have demonstrated such selection.

The failure to find substantial differences in the size of fish caught under the unrestricted and 8-in minimum gillnet mesh size regimes is not surprising. Although many studies have documented the size selectivity of gillnets (e.g., Anon. 1950, p. 7-8; Peterson 1954; Bernhardt et al. 1969; Todd and Larkin 1971; but see Lumley and Schaller 1989), this investigation did not compare the catch to the sizes of mesh used, but rather to the sizes of mesh allowed. The complement of mesh sizes used under the two regimes may not have differed markedly. Even during fall periods when mesh size is not restricted, fishers in Zone 6 often use 8-in or larger mesh to avoid the incidental catch of steelhead trout or because it would be uneconomical to maintain an inventory of nets with a variety of mesh sizes (N. K. Brigham, Zone 6 commercial fisher, Cascade Locks, OR, pers. comm. 2/89; Captain J. Johnson, Columbia River Inter-Tribal Enforcement, Hood River, OR, pers. comm. 2/89). In Zones 1-5, fishers may voluntarily deploy larger-mesh nets to avoid the

incidental catch of white sturgeon (Acipenser transmontanus) or use smaller-mesh nets to target on coho salmon during certain parts of the season (Young and Robinson 1974; J. Marincovich, President, Columbia River Fishermen's Protective Union, Astoria, OR, pers. comm. 3/89). Hence, mesh size restrictions may have little direct influence on the size of Brights caught. However, that does not mean that the mesh sizes chosen by the fishers have no selective effects on the size of Brights in the spawning run.

In the years since 1978 (inclusive) the in-river commercial fisheries have generally taken larger returning tagged Brights than were found in the escapement. This size selection agrees with observations of gillnet catches in other fisheries (Killick and Clemens 1963; Ricker 1981) and may result from fishers targeting on larger fish to maximize the value of the catch (number of fish times average weight, generally) (Kissner 1978), rather than number of fish caught. This is another example of why size of fish, as well as number of fish, should be considered in resource assessment.

The removal of the largest Brights by the fisheries can have undesirable consequences. I have shown that the fisheries also take higher proportions of females, an expected consequence of selecting the larger fish. The potential egg deposition declines as the proportion of females in the spawning run declines. Disproportionate numbers of either sex may reduce spawning efficiency by increasing the aggressive interactions that occur between members of the same sex (Chebanov 1980). A management focus on numbers harvested and escaped would overlook important differences in reproductive potential of a stock based on sex composition in the spawning population.

Another possible consequence of harvesting the largest fish, the removal of the most fecund females, probably did not occur in the in-river fisheries during the period studied. Separate examinations of the sexes showed that the fisheries generally took smaller females than were found in the escapement, suggesting that the larger, more fecund individuals escaped to spawn. The difference in effects on the sexes of the size-selective gillnet fisheries is important for

considering whether genetic changes have contributed to declining size and age. This is discussed later.

The overall (all ages, both sexes) selection differentials for size in the in-river fisheries for 1984-87 are mostly negative (i.e., the fisheries appear to reduce the average size of fish in the spawning run) among the Priest Rapids Hatchery Brights examined. However, whether the fisheries during that period were a selective force favoring genetic change to smaller size in the stock has not been proved. In an earlier section (*Priest Rapids Hatchery Environment*, p. 70), I concluded that the coded wire tagged spawners sampled in the escapement to Priest Rapids Hatchery probably were not representative of the sizes of the majority of Brights that were produced and had spawned naturally. If the natural fish are indeed larger on average than their counterparts produced at Priest Rapids Hatchery, then the selection differentials in the fisheries may be less negative or even positive (i.e., the fisheries increase the overall average size of the spawners) for the naturally produced bulk of the run, which was not represented in the estimation of selection differentials.

The sport fisheries may counter the effects of the commercial fisheries by removing more of the jacks. Although the sport fishery catches of adult Brights are small relative to the commercial catches ($\leq 10\%$ of total catch, 1984-87) (ODFW and WDF 1988, Table 27), two or three jacks may be caught in the upper Columbia sport fishery for every adult taken (LeFleur and Roler 1985; Roler and LeFleur 1986; Roler 1987). Without the sport fisheries, more jacks would probably be recovered in the escapement. Hence, excluding the sport fisheries from the run reconstruction probably causes the selection differentials for the commercial fisheries to be less negative. This potential bias tends to counter the bias resulting from possible size differences between natural and Priest Rapids Hatchery Brights.

Including or excluding jacks in the analyses of size selection by the fisheries had little effect on the results. Only in the selection differentials estimated from the run reconstruction was a substantial difference obtained by excluding jacks (Table 3). My

rationale for performing parallel analyses excluding jacks was based on the management assumption that jacks have zero fitness, i.e., that they do not spawn successfully. Although assuming size-related fitness in male salmonids is probably reasonable, I am not aware of any direct observations or measurements on Brights that would support such an assumption. The persistent presence, and sometimes high proportions of jacks in the Bright runs strongly suggests that small males do contribute to succeeding generations; if they did not, the genes favoring early maturity would be bred out of the population. Observations of other salmonid species during spawning have revealed that small males may employ strategies such as "sneaking" to participate in fertilization and thereby obtain fitnesses well above zero (Hanson and Smith 1967; Montgomery 1983; Gross 1985). Therefore I cannot support the assumption that Bright jacks are completely unfit and totally exclude them from a consideration of size selection. Hence, when weighting conflicting results of the parallel analyses, greater faith should be placed in the analyses that include all ages relative to analyses that exclude jacks. The analyses of all ages generally show greater size selection in the fisheries, because few jacks are caught relative to the number found in the escapement. Gillnet fisheries tend to be inefficient in removing the smallest male age classes (Killick and Clemens 1963; Bernhardt et al. 1969; Young and Robinson 1974).

In addition to selecting overall larger Priest Rapids Hatchery Brights, the fisheries were also found to select differently for the two sexes: larger males and smaller females were taken than were found in the escapement. I am not aware of similar or contrasting results from other studies. If naturally produced Brights of both sexes are larger than the Priest Rapids Hatchery fish used for the comparisons, then these results may not apply to the stock as a whole. There is no way to know if opposing size selection consistently occurs for the two Bright sexes in the in-river fisheries, or how such selection might be reinforced or countered elsewhere in the Bright life cycle. It is possible that males account for more of the decline in average size in the stock than do

females, with the change being propagated through generations by sex-related inheritance (see Heritability of Size and Age at Maturity, p. 43). The sexual dimorphism for size and age at maturity now seen in Brights may reflect sex-specific life history strategies that are tuned to differing selection by the fisheries as well as to the differing bioenergetic demands of gametogenesis and spawning (Holtby and Healey 1990).

The selective impact noted above applies only to very recent years and does not demonstrate whether or how the fisheries may have been selective during the earlier decades, when the apparent decline in size principally occurred. Information about the gillnet mesh sizes used during that earlier period is sparse and vague. Catches from a particular type of gillnet (diver) of 5-5/8-in. to 8-in. mesh sizes used in the lower Columbia River fishery (Zones 1-5) have been reported (Anon. 1950). In 1964, the Indian setnet fishers in Bonneville Pool used 7-3/8-in. mesh (Maltzeff 1965). Bernhardt et al. (1969) used 6-1/2-in. and 8-1/2-in. meshes in their lower river study, presumably to represent the mesh sizes commonly used for coho salmon and chinook salmon, respectively. Young and Robinson (1974) report that 7-in. to 9-in. mesh sizes were deployed for chinook salmon. For periods earlier than 1950, Wendler (1966) indicates that the only mesh restrictions were liberal minimums effective only during the summer season (June-July). Of the studies above, that by Bernhardt et al. (1969) was the only one that reported the size distributions and sex compositions associated with the mesh sizes used in the study. Even in this case, however, the stock composition of the catch and the size of the escaping Brights are not known; hence, selection cannot be estimated. Data presented by Chapman (1940) provide some of the best evidence that gillnets in earlier years (1918-40) were very selective, taking chinook salmon in August that were about 4.5 lb heavier than fish caught in traps.

Despite the knowledge that gillnets are size-selective, there are few examples of fisheries actually deploying mesh sizes that intentionally select the largest fish. Ricker (1972) described increases in proportions of jacks in three sockeye stocks and

attributed the trends to selection in gillnet fisheries. Other studies have shown that size selection by gillnet fisheries can be inconsistent and unlikely to permanently alter the average size in the stock (Killick and Clemens 1963; Todd and Larkin 1971).

The early fishers, like the present ones, had great latitude to choose the mesh sizes that yielded the greatest profit. They probably maximized their earnings by targeting the most valuable and abundant species, stock, and size of fish. Lacking better information, it is probably reasonable to assume that they used gear that generally targeted fish that were somewhat larger than average (Ricker 1981).

Conclusion I conclude that the in-river commercial gillnet fisheries can be selective for size. That they actually are or have been selective remains a reasonable hypothesis supported by evidence from recent years that selection on part of the run (coded wire tagged fish from Priest Rapids Hatchery) is occurring. Firm conclusions cannot be obtained as long as questions remain about the representativeness of samples obtained from the fisheries and escapement and about size-related fitness (e.g., what is the relative spawning success of jacks). The opposing results of size selection on the two sexes found in this analysis bear interesting implications in light of the possible sex-associated inheritance of size and age at maturity.

Natural Barriers to Migration

Three Major Barriers Prior to the era of dam construction on the mainstem Columbia River (1933 to present), upstream-migrating Brights faced at least three major natural barriers: The Cascades, The Long Narrows, and Celilo Falls (Fig. 25). The purpose of this part of the study was to determine, if possible, whether replacing these barriers with reservoirs and laddered fishways over dams changed the selective forces for size that Bright spawners encounter.

The Cascades (Rkm 236) was a vestigial natural dam caused by a massive landslide that blocked and rerouted the Columbia River 700-800 yr ago (Lawrence and Lawrence 1958). About 0.5 km long, The Cascades appears from photographs to have posed a greater barrier to passage by human voyagers than to passage by migrating salmon. The Cascades was flooded in 1938 when Bonneville Dam was closed.

The Long Narrows (Rkm 310-313), also known as Five-mile Rapids and The Grand Dalles (Strong 1959), was truly a natural wonder (Fig. 29). The renowned naturalist, John Muir (1976, p. 494, from 1888 original), describes it thus:

At the Dalles the vast river is jammed together into a long narrow slot of unknown depth cut sheer down in the basalt. This slot or trough is about a mile and a half long and about sixty yards wide at the narrowest place. At ordinary times the river seems to be set on edge and runs swiftly but without much noisy surging with a descent of about twenty feet to the mile. But when the snow is melting on the mountains the river rises here sixty feet, or even more during extraordinary freshets, and spreads out over a great breadth of massive rocks through which have been cut several other gorges running parallel with the one usually occupied. All these inferior gorges now come into use, and the huge, roaring torrent, still rising and spreading at length, overwhelms the high jagged rock walls between them, making a tremendous display of chafing, surging, shattered currents, counter-currents, and hollow whirls that no words can be made to describe. A few miles below the Dalles the storm-tossed river gets itself together again, looks like water, becomes silent and with stately, tranquil deliberation goes on its way out of the region of sage and sand into the Oregon woods.

During the May-July freshets, whirlpools up to 20 ft across (Seufert 1980) could suck floating logs entirely out of sight (F. Cramer, The Dalles, OR, pers. comm. 11/88). Upstream migrating chinook salmon observed leaving the Big Eddy immediately below The Long Narrows in the morning were caught in fishwheels upstream in a pattern that suggests migration speeds of only $50-100 \text{ m}\cdot\text{h}^{-1}$ (Donaldson and Cramer 1971). The hydraulic conditions in The Long Narrows during the

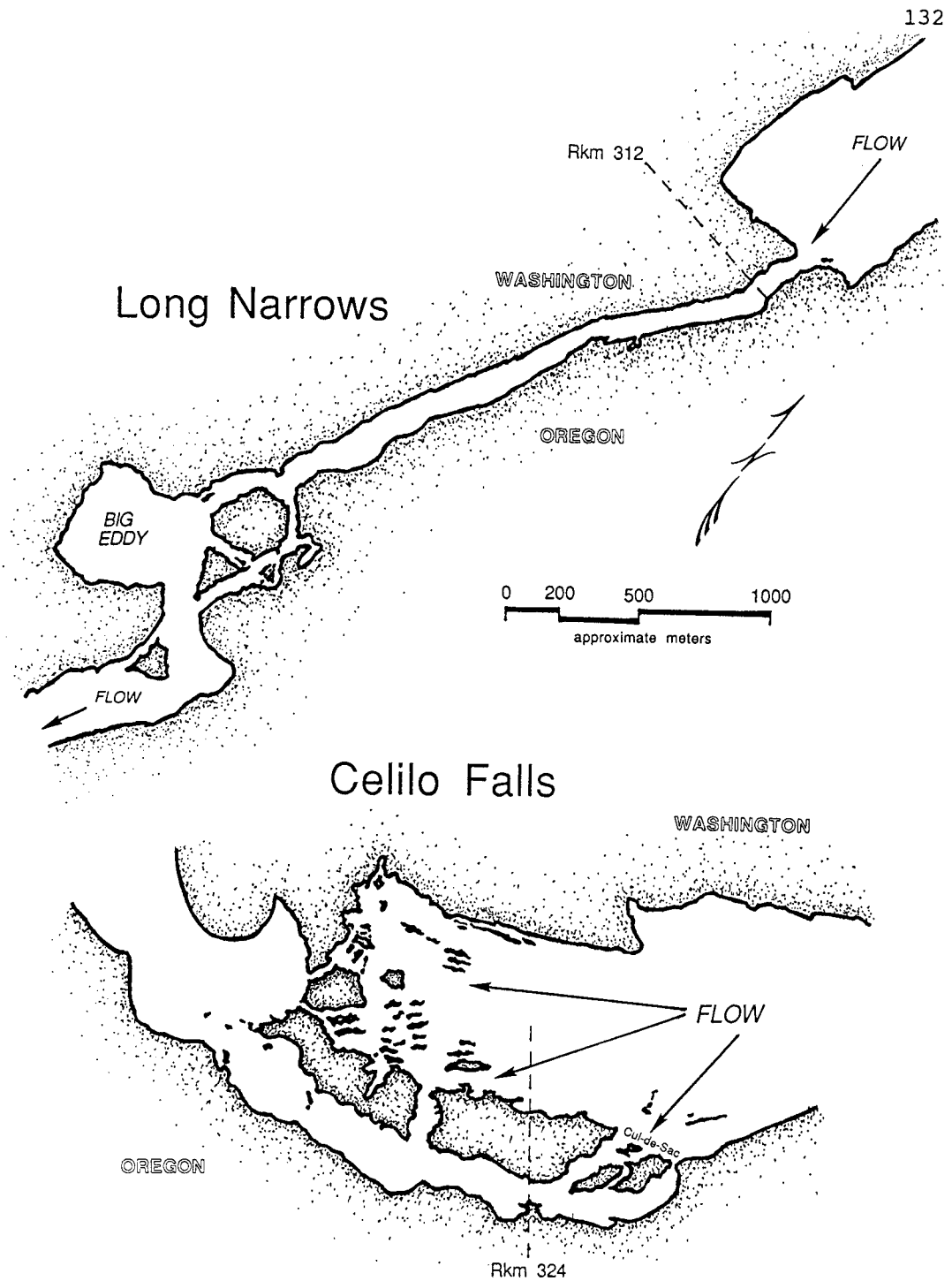


Figure 29. The Long Narrows and Celilo Falls. Redrawn from map titled "Survey of the Columbia River from The Dalles to Celilo" by R. A. Habersham, Assistant Engineer, US Engineers, September, 1874. Oregon Historical Society, Portland, OR. River kilometers (Rkm) are approximate; water levels are 4 ft above extreme low.

annual spring/summer flood not only created severe velocity and turbulence obstacles for migrating salmon, but dammed the river's flow sufficiently to submerge Celilo Falls 12 km upstream (Muir 1976, from 1888 original; Seufert 1980).

Celilo Falls (Rkm 324) was made famous in the 1940s and 1950s by its Indian scaffold salmon fishery in the late summer and fall. As the annual floods subsided, Celilo Falls emerged and funnelled the river through three principal channels (Fig. 29) that varied considerably in their passability to upstream-migrating fall chinook salmon. The cul-de-sac, on the Oregon shore, was the most upstream of the three channels and was the primary site of the Indian fishery. This channel formed an impassable shear drop during the fall fishing period (Schoning et al. 1951; F. Cramer, The Dalles, OR, pers. comm. 11/88). About 1 km downstream from the cul-de-sac was the second channel, "a large, rolling turbulent falls which [was] passable in places to the fish" (Schoning et al. 1951, p. 12). The most downstream and probably the largest of the three channels, along the Washington shore, was a system of "two deep treacherous channels" apparently branching upstream into a braided network of smaller channels and low falls (Seufert 1980, p. 38, see photos pp. 153 and 218). This channel was not heavily fished and permitted relatively easy passage (Schoning et al. 1951; F. Cramer, The Dalles, OR, pers. comm. 11/88; W. Yallup, Toppenish, WA, pers. comm. 7/30/90). Whether a Bright spawner successfully passed Celilo Falls and survived to spawn probably depended much on its time of migration and the channel it chose. Since 1957 The Long Narrows and Celilo Falls have lain buried beneath Lake Celilo, the reservoir behind The Dalles Dam.

Barriers and Fish Performance In some cases, the selective power of a river barrier is apparent in the attributes of the anadromous salmonid stocks that are native to upstream reaches. A ready example are those stocks in the Willamette River subbasin above Willamette Falls (Fig. 25). Unlike the Columbia River mainstem, flows in the Willamette formerly peaked with the winter rains of January and February, with smaller flow peaks through April (Holmes

and Bell 1960). It is believed that prior to construction of effective adult fish passage facilities at the falls and the introduction of non-native stocks, only spring chinook salmon and winter run steelhead spawned above the falls (Holmes and Bell 1960; Howell et al. 1985a,b; NPPC 1986). This contrasts with the Clackamas River, a tributary 3 km downstream from Willamette Falls, where fall-running stocks of chinook and coho salmon were present. Willamette Falls determined the nature of the stocks above it by restricting passage to only those stocks whose migration coincided with high winter/spring flows, which effectively reduce the height of the falls (Holmes and Bell 1960, see their Fig. 4 and 21).

Similar flow-dependent passability of barriers in the Columbia River from The Cascades to Celilo Falls may partially explain why the range of winter steelhead in the Columbia River extends only to The Dalles (NPPC 1986). (Recall that Columbia River flows at The Dalles and Celilo Falls are minimal in winter.) It may also account in part for the apparent genetic boundary between stocks of rainbow trout-like fishes and spring chinook salmon that occurs in the vicinity (Utter 1981; Schreck et al. 1986). As previously mentioned, this same area may have also marked the upstream limit of the range of tule fall chinook salmon.

Historical information indicates that, because of seasonal changes in flows, The Long Narrows and Celilo Falls opposed each other with regard to difficulty of passage. During the high flows of June, when Celilo Falls was flooded and probably presented little obstacle to upstream migrants, The Long Narrows was a gauntlet of turbulence and racing waters. As flows subsided through the summer and fall, The Long Narrows was transformed into a relatively placid corridor while Celilo Falls emerged as a breastwork against Bright spawners. The two obstacles did not act in unison to shape the nature of upstream chinook salmon stocks. Brights, because they passed the area during the low flows of fall, were probably impacted more by conditions at Celilo Falls than by those at The Long Narrows.

Flows and barriers can determine not only when fish may pass, but which fish may pass. Of the sockeye salmon attempting to migrate

past a natural rock slide in the Babine River, British Columbia, those that were male, larger, less mature, and less injured had greater success (Godfrey et al. 1954). The same was true for the chinook salmon in the river. The notorious 1911-14 Hell's Gate (Fraser River, British Columbia) obstruction apparently selected against females (Babcock 1914, cited by Ricker 1987), and the passability of Hell's Gate during subsequent years may have been flow dependent (Thompson 1945, 1951; Jackson 1950; but see Ricker 1947, 1987).

These observations of differential passability of barriers depending on fish traits are consistent with experimental tests of fish performance. Burst swimming speeds, which must carry the fish through short velocity barriers, are directly related to body size (Weaver 1963; Blake 1983) and decrease as the fish ripen for spawning (Paulik 1960; Powers and Orsborn 1986). The reduced swimming ability with increasing maturity probably results in part from exhaustion of energy reserves (Idler and Clemens 1959; Gilhousen 1980). Larger steelhead trout and fall chinook salmon in the Columbia River are better able to negotiate velocity barriers than their smaller conspecifics (Weaver 1963).

The height to which a fish can leap (such as at a falls) is a function of its velocity when emerging from the water⁵. Because a leaping fish probably accelerates only over a very short distance (Stuart 1962), its emergent speed is probably less than burst speed. Nevertheless, larger fish leap higher than small fish, provided the plunge pool is adequately deep (Stuart 1962).

Given this information, I hypothesized that the Columbia River barriers described above probably selected for large size and that fishways, which replaced the natural barriers, are less size-selective. Tests have indicated that ascending well designed

⁵ The leap of a fish has a parabolic trajectory with maximum height (h) of $0.5(v \cdot \sin\theta)^2 \cdot g^{-1}$, where v is emergent speed, θ is the angle of leap from horizontal, and g is the downward acceleration of gravity ($980 \text{ cm} \cdot (\text{sec}^2)^{-1}$). Adapted from Powers and Orsborn (1986).

fishways may be relatively easy for adult salmonids (Collins et al. 1962). Some fish may have difficulty entering and remaining in adult fish passage facilities, and some may fall back over the dams (CBFWA 1991), but there is no indication that these problems are related to fish size.

Size-related Passability of Natural Barriers in the Columbia River Unfortunately, there appears to be no way to determine whether small fish were better able to complete their spawning migration once the natural barriers were replaced with fishways at dams. Counts of fall chinook salmon passing McNary Dam increased dramatically when The Dalles Dam was closed and The Long Narrows and Celilo Falls were flooded (Fig. 25 and 30). Although elimination of the Celilo Falls fishery undoubtedly accounts for much of the increase, it is possible that many small fish formerly denied passage at Celilo Falls in the fall season were able, beginning in 1957, to migrate as far as McNary Dam and upstream spawning areas. However, the proportion of jacks (representing small fish) in the fall chinook salmon run at McNary Dam actually shows a decrease from 1956 to 1957 (Fig. 30). This contrary decline, which suggests that small fish were better able to migrate upstream before The Long Narrows and Celilo Falls were flooded, results in large part from a change in the jack cut-off length from 24 in. (1955-56) to 18 in. (1957)⁶. Dam counts can be unreliable for other reasons (Fredd 1966). Hence, counts of chinook salmon passing McNary Dam are not suitable data for testing the hypothesis that inundation of The Long Narrows and Celilo Falls facilitated the upstream passage of small Brights.

Some circumstantial evidence suggests that small Brights may have been impeded by the hydraulic conditions at Celilo Falls. Fall chinook salmon caught by Seufert Bros. seines on the gravel bars below the falls were of smaller average weight than those caught by

⁶ The present cut-off length of 22 in. was apparently adopted in 1964, concurrent with the change at Bonneville Dam (USACE 1964).

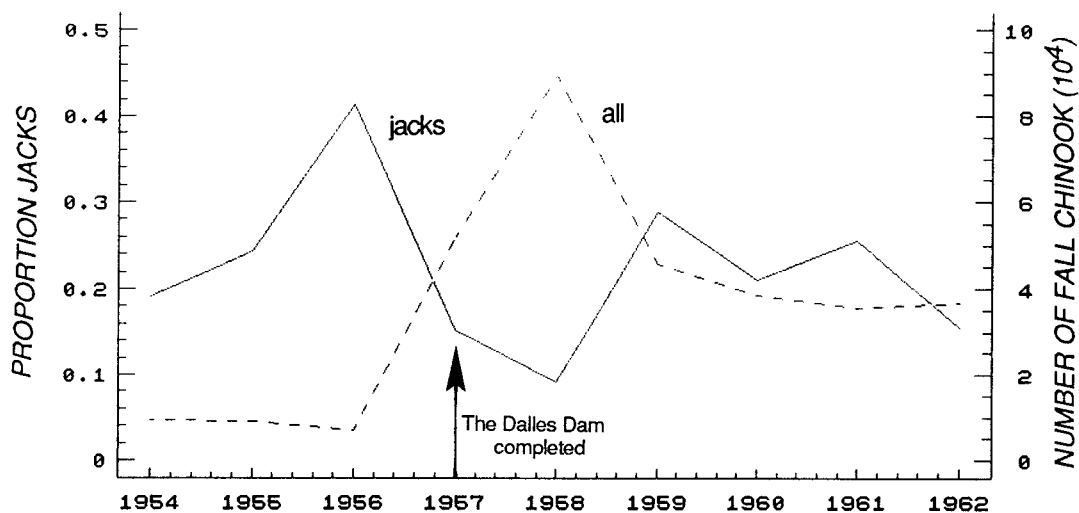


Figure 30. Total number of fall chinook salmon (mostly Brights) and proportion that was jacks passing McNary Dam during September and October in years before and after closure of The Dalles Dam downstream in 1957. All fish less than 18 in. (45.7 cm) in length were classified as jacks, except for 1955 and 1956 when a cut-off length of 24 in. (61 cm) was used. Data from USACE (1954-62).

Indian dipnets at the falls itself in mid-September 1949 (Schoning et al. 1951). Over half of the male chinook salmon in a sample of the seine catch butchered at Seufert Bros. Cannery in The Dalles on 10 September, 1950, were jacks (the criterion for jack classification was not reported) (Anon. 1950). Although these reports suggest an accumulation of smaller fish below the falls, such results could also arise from seine fishing in areas used more often by smaller fish during upstream migration (e.g., the shallows adjacent to gravel bars), or from other biases.

While some routes over Celilo Falls were no doubt impassable or inhospitable to Brights of all sizes and particularly to the smaller, there may well have been factors that influenced which route a Bright of a particular size chose to attempt. Able to detect small differences in velocity (Bell 1986), upstream migrating salmonids are generally attracted by water of higher speeds (Stuart 1962; Seufert

1980; Bell 1986). The routes chosen over obstructions also vary according to flows and fish size (Stuart 1962); hence, small Brights may have been more (or less) attracted to the readily passable Washington-side channel of Celilo Falls. Although the choice of an impassable route was not strictly irreversible, the intensive dipnet fishery around the Oregon-side channels may have exacted a high toll from the fish attracted to those areas. How the Brights of different sizes responded to the cues at Celilo Falls and chose their routes probably had as much influence on the successful passage of fish as did their swimming and leaping abilities. Both the route chosen and the ability to pass upstream via that route may have been a function of size, but that remains an untestable hypothesis.

Temperature In addition to waterfalls and other obvious barriers to migration, water temperature may impede upstream passage and have a size-selective effect on migrating adults. As already noted, Lake Roosevelt and other large storage impoundments have shifted the thermal cycle of the Columbia River so that the high temperatures of summer occur later (Jaske and Goebel 1967), during the migration of Brights. Columbia River temperatures commonly exceed 21°C (70°F) during August (Collins 1963; Shew et al. 1985; Meyer 1989), and a high of 23.9°C (75°F) was measured at Bonneville Dam 13 August 1990 (unpubl. data from B. P. Lumley, Columbia River Inter-Tribal Fish Commission). These temperatures equal or exceed incipient lethal temperatures that have been measured for Columbia River steelhead and chinook salmon stocks migrating during the hottest seasons, and "ecological death" due to equilibrium loss occurs at even lower temperatures (Coutant 1970).

Fish of various sizes are not necessarily equally vulnerable to the adverse effects of high temperature. Smaller jack chinook salmon (probably of the late summer-run stock in the mid-Columbia) were more resistant to temperatures of 24°C and 25°C than larger jacks in laboratory studies (Coutant 1970). Smaller Brights may be better able to endure the high temperatures that now occur during their

migration, and such selection for small size may have contributed to the decline in average size.

Conclusion Obstacles such as Celilo Falls had the potential to be a selective force for large size in Brights. However, passage at the falls was not uniformly difficult, the choice of an easy passage route may have been size-related, and there is a dearth of useful data for demonstrating a change in fish size coincidental with inundation of the barriers. I can only say that replacing natural obstacles with well designed adult fish passage facilities at dams should have (based on the physics involved) allowed smaller Brights to spawn successfully and contribute to declines in average size and age in the run. Higher temperatures during the spawning migration may have a greater impact on larger fish and contribute to lower average size in the run.

Spawning

The life cycle closes as the Brights spawn. Spawning conditions for Brights have changed in the last six decades, and selection for size by the spawning environment probably has also changed. Some of those changes have previously been described in sections on *Maternal Influences* (p. 50) and the *Hanford Reach Environment* (p. 65). This section considers the relationship between the size of Bright spawners and their spawning environments, both natural and artificial, and how changes in the environment might favor spawners of smaller size. The working hypotheses are: (1) the physical and biological conditions during, and at the site of spawning can be selective for size, and (2) changes in those conditions now favor spawners of smaller size than previously. Because I have been unable to find data directly relating to these hypotheses, coverage will be limited to discussion.

Spawning in the Hanford Reach

Previous coverage of the Hanford Reach environment centered on known hydraulic and thermal changes that have occurred in the Hanford Reach since development of the hydroelectric system. Some of the ways that the reproductive fitness of females of differing sizes may have been affected by these changes were discussed, and they merit restatement here.

If smaller females tend to spawn in shallower water, for whatever reason, then they may now enjoy greater fitness than previously (i.e., more of their progeny would be likely to survive). Two of the possible reasons that smaller females might spawn in shallower areas are (1) competitive exclusion from deeper areas and (2) the possible occurrence of habitat more desirable to smaller females in shallower areas (e.g., smaller substrate sizes and lower water velocities). Redds placed in shallow water are now less likely to be destroyed by natural winter drought, freezing, and ice scouring. Since implementation of the Vernita Bar Spill Agreement in

1988, shallow-water redds are also less likely to be dewatered for perilously long periods due to fluctuations in the discharge from Priest Rapids Dam (FERC 1988). There is presently, however, no evidence that spawners using deeper or shallower areas differ in average size.

A delay of approximately one month in the thermal cycle of the river may also favor smaller females. Smaller Brights presently tend to run (*In-river Fisheries*, p. 110) and spawn (Spawning Time, p. 51) later than the larger fish, perhaps making them and their progeny less vulnerable to undesirably high early-season temperatures. Some circumstantial evidence supporting this hypothesis comes from the former Rocky Reach Spawning channel, where the female Bright prespawning mortalities averaged about 4 cm (FL) longer than females that spawned (Meekin et al. 1971). Large fish may not tolerate adversely high temperatures as well as smaller fish (Coutant 1970). We do not know with any certainty whether changes in the thermal and hydraulic regimes of the Hanford Reach have shifted selective factors in favor of small spawners.

One biological factor was previously mentioned as a possible selective agent for size during spawning: size-related dominance. Females must establish and defend a territory for their redds, but their success may be unrelated to their size (Hanson and Smith 1967; Schroder 1981). Between 1947 and 1987, the numbers, and presumably the densities of Bright redds in the Hanford Reach and Vernita Bar increased markedly (Watson 1970; Chapman et al. 1986). If large females had any competitive spawning advantage during the higher densities, such advantage was not reflected in the declining average size during the same period (Fig. 8). It is unknown whether the competitive environment on the spawning grounds has contributed to, or buffered declining size in the stock.

Male Brights, however, may be more subject to behavioral selection for large size during spawning. Dominance for mating position is size-dependent, and there is evidence that female spawning behavior is sensitive to the size of attendant males (Hanson and Smith 1967; Schroder 1981; Hankin and McKelvey 1985; Foote and

Larkin 1988). However, smaller males can retain some fitness by sneaking fertilizations (Hanson and Smith 1967; Schroder 1981; Gross 1984). The strength of selection for large male size is probably a function of the relative abundance of the two sexes; the greater the ratio of males to females, the more likely that size selection is operative (Schroder 1981). Sex ratios of naturally spawning Brights, available for only a few recent years, have been close to unity (Appendix Table D.5, but note 72.7% females in 1981), which reduces the likelihood of intense selection for male size in those years. There is little reason to suspect that behavioral selection during spawning has been a factor in the decline in average size of Brights, although it is possible.

Failure to demonstrate that changes in the natural spawning environment are related to the decline in size and age does not mean that the environmental changes have not been contributing causes. More importantly, it does not mean that spawner size is independent of the spawning environment. Before considering the artificial spawning environment at Priest Rapids Hatchery it is necessary to more closely examine how existing spawning conditions in the Hanford Reach may influence spawner size.

Spawning in the Hanford Reach is remarkable for several reasons. It has long been recognized that Brights sometimes spawn at relatively great depths (Anon. 1947; Edson 1957; Meekin 1967b; Watson 1970), and it is now known that extensive spawning occurs even below 5 m (Chapman et al. 1986; Swan et al. 1988). This deepwater spawning often occurs in large substrates (10-20 cm [4-8 in] rubble and 20-30 cm [8-12 in] rock) and relatively high velocities ($> 1 \text{ m s}^{-1}$) (Swan et al. 1988). Redds are uncommonly large (Bauersfeld 1978; Chapman et al. 1986), particularly when considering that large substrates and high water velocities are expected to depress redd size (Burner 1951).

Why Brights spawn at great depths is a question that is still unanswered. Water level fluctuations have been offered as an explanation for an early observation that few Brights spawned on shallow gravel bars that would be ideal for spring chinook salmon

(Anon. 1947). D. Chapman (Don Chapman Consultants inc., Boise, ID, pers. comm. 1/89) hypothesizes that winter drought and ice scour accompanying freeze-up during incubation selected against spawning in shallow water. If so, deepwater spawning would be adaptive, and large size and great strength may have been required for spawning in the mid-channel depths where water velocities and substrate size may be greater (Swan 1989). Cleaver (1969) speculated that the large spawning substrates in the Kalama River (tributary of the lower Columbia River) have selected for the large females typical in the run of fall chinook salmon to that stream. Ricker (1980) suggested that large female size may be required for chinook salmon to spawn in the large substrates of swift reaches such as the Harrison River Rapids (Fraser River system, British Columbia).

Although it is obvious that large females have the advantage where high water velocities and large substrates prevail, why would large Brights preferentially spawn in those areas when smaller substrates (10-20 cm gravel) and slower velocities ($< 1 \text{ m s}^{-1}$) are also available, but little used, in the Hanford Reach (Swan et al. 1988)? The answer may lie in survival advantages to embryos and fry that incubate in the large substrates of the Hanford Reach. Although not consistent, available evidence indicates that large substrates may provide greater permeability to flows and easier emergence for fry than smaller substrates (Chapman 1988). Larger substrates may also be less easily disrupted during high flows (pers. comm. with C. D. Becker from Swan 1989). Large female size may have been, and may still be a requisite for exploiting favorable incubation habitats in the Hanford Reach.

High water velocities and large substrates in mainstem spawning areas are one possible explanation for correlations that have been noted between river size and average fish size and age. Schaffer and Elson (1975) attributed a correlation between mean age at first spawning of North American stocks of Atlantic salmon and length of the natal river to the energy demands of the upriver migration; longer streams require more energy to ascend. Scarnecchia (1983) found a similar relationship in Icelandic stocks of Atlantic salmon

where percent of grilse was inversely related to river length and discharge. However, he rejected the energy-requirements hypothesis of Schaffer and Elson (1975), based on evidence that the oldest and largest fish more often spawned in the lower main channels. High flow velocities in the mainstem areas can deposit large substrates (Chortley et al. 1984, Fig. 12.14) that are usable by only the larger female spawners.

In summary, naturally spawning female Brights often choose deep sites in relatively large substrates and high velocities. The reasons for the choice are unknown, but may be related to the formerly low winter flows and/or to the relative favorability of particular substrate and velocity microhabitats. Large females, better able to spawn in large substrates and high velocities, may be favored by spawning conditions in the Hanford Reach. Large males are favored by biological factors during mating and spawning, but whether their fitness is substantially higher than small males is unknown. It is not known whether changes in the conditions in the Hanford Reach have favored smaller spawners and contributed to the observed declines in size and age. The persistence of larger and older fish in the stock suggests that selection for large size, perhaps in the spawning environment, is counteracting the selection against large size and old age in the fisheries.

Spawning at Priest Rapids Hatchery

The application of artificial spawning methods represents probably the most significant change in the spawning environment of Brights. The methods practiced at Priest Rapids Hatchery can impact the size and age structure of the stock in at least five ways: (1) changing the composition of spawners in both the natural and the hatchery populations by transplanting natural spawners of selected sizes to the hatchery, (2) importing exotic genetic material from other stocks or substocks, (3) eliminating the natural volitional mate selection process, (4) changing physical size-selective factors

that influence the fitness of spawners, and (5) reducing the effective population size of the stock.

Selective broodstock trapping in the left fish ladder at Priest Rapids Dam, initiated in 1963 to obtain seed spawners for the Priest Rapids Spawning Channel, has been a common practice. The objective of the trapping in years when volunteer spawners were abundant was to ensure that genetic material from the natural stock was included in the hatchery program (L. Atkins, Resource Manager, Salmon Culture, WDF, Olympia, WA, pers. comm. 12/14/89). Hatchery personnel trapping at the dam have targeted on adults (usually fish > 69 cm [27 in] long), particularly females (B. Ault, WDF, Soleduck Hatchery, pers. comm.). Because the trapping has taken a substantial portion of the adults passing over Priest Rapids Dam in some years (Fig. 19), it has sometimes exacerbated the already large proportion of jacks in the upstream escapement (Fig. 31).

The trapping of large brood stock has, if anything, probably helped maintain the average size of Brights produced by Priest Rapids Hatchery and may have ameliorated any reduction in size and age at maturity caused by the favorable rearing conditions for juveniles at the hatchery (see *Priest Rapids Hatchery Environment*, p. 70). The toll for the removal of large spawners at the dam has undoubtedly been paid by the upstream substocks, which in some years (e.g., 1963-70, Fig. 31) were probably left with mostly jacks, a few adult males, and even fewer females for spawners. In 1963, 92% of the fall chinook salmon passing Rock Island Dam were classified as jacks (Laramie undated). Such unbalanced sex ratios may reduce reproductive success (Chebanov 1980; but see Killick and Clemens 1963), as might the small size of the spawners if large size is adaptive. The substocks above Priest Rapids Dam are not believed to make large contributions to production of the stock as a whole, perhaps due in part to the broodstock trapping; hence, it is unlikely that any changes in size of this portion of the stock had an impact on the overall average size and age of Brights.

Importing exotic stocks or substocks could contribute to size and age changes if the genetic basis for size or age at maturity in

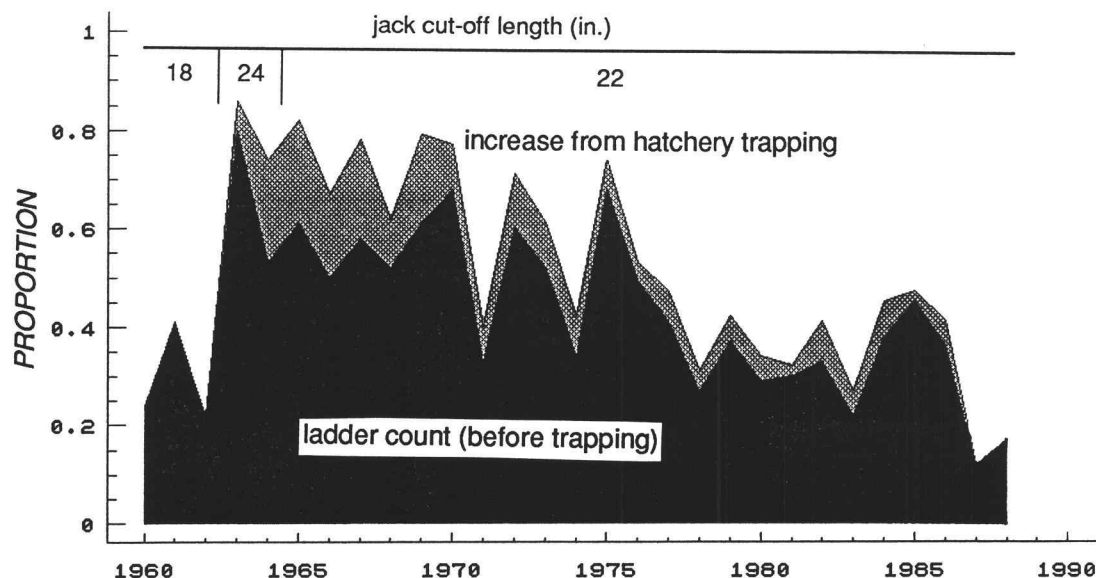


Figure 31. Proportion of the fall chinook salmon run (mostly Brights) at Priest Rapids Dam that was classified by length as jacks (solid area) and the increase in proportion of jacks in the escapement caused by selective removal of adults at the dam for brood stock at Priest Rapids Hatchery (cross-hatched area). Data provided by M. Dell, Public Utility District No. 2 of Grant County, Ephrata, WA.

those groups differed from the Hanford Reach and Priest Rapids Hatchery Brights. Extensive imports have occurred, particularly from the egg bank program for Brights at Bonneville Hatchery. Brood stock for the Bonneville egg bank has been obtained mostly by trapping at Bonneville Dam (Howell et al. 1985a); hence, it is a genetically heterogeneous mixture of Bright substocks from the Deschutes, Snake, and mid-Columbia (including the Hanford Reach) rivers. The Snake River substock was also hybridized with the Priest Rapids stock at Rocky Reach Hatchery in the mid-1980s (Hill 1984; Kirby 1985). Although there is weak evidence that the Snake River substock may have smaller average size (Utter et al. 1982), it is unknown whether this mixing of substocks has contributed to a smaller size in the Brights. Tule fall chinook salmon have also been transplanted into the mid-Columbia (Smith 1966; Howell et al. 1985a; Dauble and Watson

1990), but there is no evidence that sustaining populations were established (except perhaps in the Yakima River; Howell et al. 1985a). Because of differences in spawning time, interbreeding between Brights and tules was probably minimal. Past stock and substock importation is not a likely cause of size changes in Brights.

Artificial spawning replaces natural sexual selection with intentional or unintentional selection by hatchery personnel and trapping facilities. Given the complexities of spawning behavior and how little is known about mate selection mechanisms, hatchery practices cannot duplicate the natural spawning regime (Helle 1981). The potential role of size in mate choice among naturally spawning salmonids was discussed earlier. Until 1988, jack Brights were spawned at Priest Rapids Hatchery only when there was a shortage of adult males (B. Ault, WDF, Soleduck Hatchery, pers. comm.), so intentional selection for large size was occurring, at least in males. Since then, however, jacks have been included as 2% of all spawners (male and female) in accordance with Seidel (1983) (P. Pedersen, Manager, Priest Rapids Hatchery, pers. comm.). There is no record of intentional size selection for females. The rationale behind the guideline to spawn jacks is reasonable; it assumes that they represent an important part of the genetic diversity in a stock, most notably genes for rapid growth. However, specifying that 2% of the spawning stock should be jacks is purely arbitrary; they probably spawn in nature but their relative success is unknown. If no jacks had been spawned at the hatchery in the past, we might expect that the change in practice would contribute to reduced size and age of the hatchery component of the run in subsequent years, but we do not know whether the specified 2% is proportionately more jacks than were previously spawned, on average, at Priest Rapids Hatchery. It does not appear that selection for large size during hatchery spawning has contributed to the change in average size.

Whether artificial spawning has eliminated natural physical factors favoring large size is not known. Earlier sections have considered how the natural spawning environment might select for

large female size, and it is obvious that these factors do not exist in the hatchery. There is no substrate or water velocity during spawning, and all eggs are incubated in the same continuous supply of 12°C water. All eggs have the same opportunity to develop regardless of maternal size. If physical factors in the spawning environment were known to favor larger females or their embryos, then we might conclude with some certainty that artificial spawning and incubation was contributing to a reduction in Bright size. However, this remains simply an intriguing hypothesis.

Hatchery spawning practices could also contribute to smaller average size if those practices reduced the effective population size and random genetic events led to higher frequencies of genes for small size. However, it is unlikely that the operation of the hatchery has had sufficient negative impact on the effective population size of the entire Hanford Reach/Priest Rapids stock to precipitate such an event. Priest Rapids Hatchery can remove from the natural population only those fish passing above the primary spawning area in the Hanford Reach, where more than 30,000 adult Brights are estimated to have spawned in each of the years 1986 through 1990 (TAC 1991). Hatchery fish composed less than 20% of the adult Brights returning to the mid-Columbia above the confluence of the Snake River in those same years (TAC 1991, derived from Tables 9 and 10 in chapter on fall chinook salmon). Spawner numbers are well above effective population sizes at which random genetic events would be significant.

In summary, it seems unlikely that the spawning practices at Priest Rapids Hatchery have played a role in the declining size and age of the stock. However, so little is known about the selectivity of the natural environment that we cannot be certain that artificial spawning is not imposing radically different selection for spawner size. Selective spawning of adult (large) males may actually counteract to some degree the forces, such as accelerated development of juveniles at the hatchery, that favor early maturation and small size. We must also remember that Brights have been artificially propagated only in the last three decades, so hatchery practices

cannot be responsible for the large declines in size that apparently occurred before then. Hatchery practices are less likely to cause major changes in the stock as long as the majority of the run is produced naturally, although hatchery production will probably increase proportionately in years ahead.

Causes: A Concluding Discussion

The purpose of this discussion is to bring together the many results and ideas from the preceding coverage of potential causes of size and age declines in Brights. In addition to providing an overall synthesis of results, I will briefly consider the value of such a broad life-cycle approach to understanding changes in life history patterns. The implications of these results for management will be described in a later chapter.

Two models were used to initiate the investigation of potential causes for changing size and age at maturity. The Causal Sphere model, with its multiple layers and interactions, captures the complexity of the problem. I have used this model to identify and investigate potential causes for change in average size of Brights. A mathematical model could serve the same purpose, but its very explicit nature demands better quantitative information on influential factors and their interactions than was available for this broad problem. This investigation of potential causes for declines in average size of Brights has produced a clearer picture of how some activities may influence certain important life history traits and has illuminated gaps in our understanding of Bright biology.

Size- and age-selective fisheries, in the ocean and in-river, are probably important contributors to declines in size of Brights. This conclusion is supported mostly by evidence of selection in recent years, the knowledge that exploitation rates and selectivity were probably higher in the decades before the stock was decimated (and good data were gathered), and similar conclusions by other researchers investigating demographic changes in salmonid stocks (e.g., Van Hyning 1973; Schaffer and Elson 1975; Ricker 1972, 1981).

Some researchers have concluded differently. Healey (1986) and Riddell (1986) argued that fisheries impose only a small fraction of the total mortalities borne by salmonid stocks through the course of their life cycle, and therefore are not likely to have a great impact on stock genetics. This argument, however, assumes that the trait of

interest is equally subject to selection throughout life. But size and age at maturity are most fully expressed and subject to direct selection in the later life stages when fisheries occur. Selection on a correlated trait (indirect selection) during some early life stage probably does not have as great an impact on size and age at maturity in subsequent generations as direct selection on those traits.

The impact of a selective force, such as a fishery, is related to the proportion of the reproducing population that is affected, not to the proportion of the population alive at the beginning of the generation. For example, if 10 individuals of a family of 5000 survive to mature and a fishery takes the largest eight of those, then the fishery contributes only a meager 0.16% of the total lifetime mortalities. However, and more importantly, the fishery killed 80% of the potential spawners and imposed intense selection for size. Still, the nature of the fishery impacts can be estimated in only a crude way, because it is not known what the natural fitness of the fish would be in the absence of the fishery. For example, if the eight fish taken by the fishery would have otherwise failed to reproduce, then the fishery had no genetic impact. Conversely, if the only viable spawners were among the eight fish captured, then the fishery effectively extinguished the family. This is the extreme case of how countervailing selection reduces productivity. Considering that the natural fitness of the fish is unknown, then the most reasonable approximation is to assume equal fitness (likelihood of producing quality offspring) for all those alive at the time of the fishery. The expected genetic impact of the fishery, then, is related to the intensity of selection on the existing population. The proportion of the lifetime mortalities contributed by the fisheries is irrelevant for assessing genetic impact.

The foregoing example of the effects of a selective fishery underscores the important role of countervailing selection. Considering the heritability of size and age at maturity, and the apparent intensity of selection by the fisheries, I would interpret the perseverance of older ages and larger sizes in the Bright runs as

evidence that countervailing selective forces are indeed operating on size and age at maturity (Healey 1986). The natural spawning environment, for example, may be exerting forces that counteract selection by the fisheries. Countervailing selective forces on size and age may mitigate each other's impacts on the traits, but the opposing forces may totally destroy a stock's reproductive potential.

Artificial propagation is probably another contributing cause of the change in size. Although Priest Rapids Hatchery has commonly selected for large size (high age at maturity) in its brood stock, I found evidence of earlier maturity and smaller average size in known hatchery Brights relative to fish that were apparently produced naturally in the Hanford Reach. Favorable growth conditions during early rearing are the most likely reason for the difference, although the two incubation environments may select differently for traits correlated with parental size (e.g., egg size, spawning site).

Hatchery production can also work in conjunction with harvests to produce major changes in life history patterns. High egg-to-adult survival of hatchery fish, attributable principally to high egg-to-smolt survival, can facilitate impacts by selective fisheries by allowing higher exploitation rates and hence more intensive size and age selection. With ocean fisheries intensively selecting for low age at maturity and the hatchery selecting for large size in its brood stock, it would not be surprising, after a few generations, for the stock to show more rapid growth and earlier maturity at relatively large size-at-age (the largest individuals among the youngest age classes would be more fit under this selection system). Indeed, a shift to earlier maturity and larger size at age occurred in the Spring Creek tule stock of fall chinook salmon, which was subjected to such a selection system for a few generations before its collapse (Junge and Phinney; Cleaver 1969; Henry 1971; Van Hying 1973).

Development of the Columbia River has wrought major changes to the freshwater environments of Brights, but it is not at all clear how those changes may have influenced size and age at maturity. Some mechanisms that might have contributed to the declines were

identified, but it could also be argued that prevailing spawning and rearing conditions favor large size and may have opposed the declines. Changes in ocean rearing conditions appear to be the opposite of what would be expected to contribute to declining size and age.

Although I have emphasized causes related to genetic selection, the apparent decline in size of Brights may also be the result of processes unrelated to heredity. Increases in exploitation rate and other sources of mortality can shift the age and size structure downward (Ricker 1975). Changing growth conditions may produce shifts in age (hence size) at maturity (Miller 1956, 1957; Power 1986). By reducing the numbers, and possibly the fitnesses of spawners, fisheries can cause early maturity by improving growth during life stages when limiting resources would otherwise inhibit individual growth. However, the strength of density effects on growth is unknown for Brights. The principal ways that environments influence size and age at maturity were identified and described earlier (see Relevance of Theory to the Study Problem, p. 8). Considering the heritability of the traits, it is unlikely that such a long-term trend would not reflect and impact the genome of the stock. As Ricker (1981, p. 1637) states,

... any hereditary effects of man's selection on the size of the fish in wild stocks have for the most part remained unknown, although this does not necessarily mean that they have been unimportant.

This study made a comprehensive examination of available knowledge in an attempt to determine the causes of an apparent downward trend in the size at maturity of Brights. Fisheries, hatchery practices, and changes accompanying development of the Columbia River were identified as probable causes of the trend, which may well reflect genetic changes in the stock. Numerous obstacles were encountered in the investigation. An incomplete knowledge of the ecology and general biology of Brights poses probably the most important problem in detecting selection (Endler 1986; Nelson and Soule 1986). The complex life cycle and tetraploid genome of Brights

make this doubly true. The question of what factors have the greatest impact on size and age at maturity of Brights is a riddle that is likely to remain unsolved.

CONSEQUENCES OF CHANGES IN SIZE AND AGE

Why should fishery managers be concerned about declining size and age in Brights? Size and age declines can impact the commercial value, reproductive potential, and adaptive capacity of a stock. These three areas of concern overlap.

Arguably, the commercial value of a stock is the primary reason that we are interested in the other two; the present and anticipated ability of Brights to generate or conserve wealth motivates humans to invest in their management. "Commercial value" here refers to the monetary benefits that are directly or indirectly obtained from the resource. Intrinsic, ceremonial, religious, subsistence, recreational, ecological, and other values associated with a resource such as Brights usually receive political/management attention only to the extent that they can be translated into monetary benefits: revenues received and/or costs avoided. Therefore, I will emphasize the commercial significance of declining size and age. Previous chapters have briefly touched on some of the impacts potentially associated with the trend, and I will now explain the consequences in more detail.

Commercial Value

Brights are presently managed principally for harvest in commercial and recreational ocean and in-river fisheries. The value of the commercial catch is fundamentally a function of biomass landed, i.e., number of fish times average weight. Because most present harvest allocations for salmon specify numbers of fish, the size of the fish becomes very important in determining the benefits derived. For example, assuming that the average weight of Brights declined 2.7 kg (6.0 lb, approximately 25%) during the 68-yr period from 1918 to 1986 (see CHANGES IN BRIGHT SIZE AND AGE AT MATURITY, p. 31), then the average value of each fish caught in the in-river fisheries declined by 0.25, thereby compounding the loss in revenues associated with drastically fewer fish caught. Larger salmon are

also more valuable because they often demand a premium price. Around the turn of the century, chinook salmon weighing more than 25 lb fetched one or two cents (10%-20% based on 1900 prices) per pound more than the smaller fish (Smith 1979). Premiums are still paid for large chinook salmon caught in many troll fisheries⁷.

Losses in average size can be compensated for, at least in part, by increased numbers. Unfortunately, numbers of Brights have probably also waned concurrently with the apparent decline in size (see Recent Historical Context, p. 16). Also, because of size premiums, a given biomass of many small fish would not be equivalent in value to the same biomass of a few large fish.

The obvious economic consequences of smaller average size have been acknowledged by others (e.g., Killick and Clemens 1963; Healey and Heard 1984), yet managers of salmon fisheries have been reluctant to use anything more than simple counts of fish when allocating and accounting for harvests. The result is that fishers, and the organizations that represent them and regulate their fishing, can maintain or increase the value of their allowable catch by landing only the largest fish. Such "high-grading", to be discussed further in the next chapter, can thwart efforts to conserve and equitably allocate the resource.

Commercial fisheries are not the only users of Brights that place a premium on large size. Recreational users -- whether fishers, viewers, or those that merely appreciate the fact that Brights exist -- undoubtedly consider a 30 lb fish superior to one (or probably even 10) that weighs only 3 lb. Tribal subsistence fishers at Celilo Falls often did not even retain the smallest fish they caught (USFWS 1953, 1954), and it is unlikely that an equal weight of many small fish would have the same cultural value for many other tribal purposes as would a single large fish. Fish size is an important determinant of its value, even for users other than commercial fishers.

⁷ E. Critchlow, Portland Fish Wholesale Co., Portland, OR, pers. comm. 6/90; D. Gaudet, Commer. Fish Div., Alaska Dep. Fish Game, Juneau, AK, pers. comm. 6/90.

Reproductive Potential

Selection on a trait such as size can make a stock less well adapted to its environment, thereby diminishing its ability to reproduce (Hershberger 1976a; Kapuscinski and Jacobson 1987). Large fish probably contribute more per fish to the perpetuation of the stock. The greater fecundity of large females is well-documented (e.g., Rich 1925; Rounsefell 1957; Mathews and Meekin 1971); when large fish are absent in a spawning stock, the potential egg deposition is reduced. Large females also may be better adapted for spawning in the natural environment, and their initially larger progeny may survive better (see *Maternal Influences*, p. 50). The potential for increased survival for the offspring of large females, as yet unproved for Brights, means that stock productivity could suffer from far more than a simple reduction in fecundity when average size declines. Whether stock productivity has lagged concurrently with the apparent decline in average size is unknown; efforts to measure the production of naturally spawning Brights with data presently available have failed (Rogers and Hilborn 1988).

The size of males may also impact stock productivity. Although smaller males are fully capable of fertilizing the spawned eggs in the absence of larger males, small sires could result in female progeny that are smaller and possibly less fit. Hence, sexual selection for large male size (Hanson and Smith 1967; Schroder 1981; Hankin and McKelvey 1985; Foote and Larkin 1988) may be an evolutionary adaptation to size-related fitness in females.

When considering the adverse consequences of lower size and age, we must be mindful that the phenotypes of returning spawners have proved to be fit in all the environments encountered thus far in their life cycle. If spawning fish tend to be small or young relative to the phenotypes of fish removed by the fisheries and other factors, then small size and/or early maturity were adaptive and may be necessary for perpetuation of the stock, given the same set of environments, including fisheries. It is not known which phenotypes

are better adapted for spawning and which ones can, through maternal influences, maintain higher fitness into the next generation. However, we already know that large fish have greater commercial value; if we suspect that large fish also have greater net reproductive value and/or carry part of the stock's adaptive capacity, then it would be desirable to control the size- and age-selectivity of factors (e.g., fisheries and hatchery practices) known to impact those heritable traits.

Early maturity may benefit stock productivity in some special situations. Donaldson and Menasveta (1961) used selective breeding for early maturity, rapid growth, and other traits to produce a run of chinook salmon that had a high return rate to the hatchery. However, the fishery contributions were not accounted for, and much of this stock's high survival may have resulted from eluding harvest by maturing early. This stock was also not subjected to selective forces in a natural spawning environment, which may have resisted the selection imposed by the researchers. Anyone propounding early maturity as beneficial for the production of a predominantly natural stock such as Brights must first address the negative impacts to the fisheries, the lower fecundities resulting from smaller size, and the potential obstacles faced by smaller spawners in the natural spawning environment.

The ability of the Bright stock to support future harvests is probably handicapped by the selective removal of the potentially largest fish and the resulting decline in average size of escaping spawners. However, except for counting solely adults (jacks are excluded), managers do not consider the reproductive potential of the spawners when setting escapement goals. Management practices that consider, when accounting for harvests and escapement, a 3-yr-old male equivalent to a 5-yr-old female laden with 5,000+ eggs are not sound. Alternative methods of measuring harvest and escapement are discussed in the following chapter.

Adaptive Capacity

The adaptive capacity of a stock, its ability to persist as environments change over the years and generations, is dependent largely on the diversity of its life history types. Computer simulation modeling has demonstrated that, in variable environments, populations show greater variability in numerical abundance and have greater potential for extinction when they are deprived of life history types (Hirai 1987). As discussed earlier (Relevance of Theory to the Study Problem, p. 8), a range of ages and sizes at maturity contributes to the stabilizing life history diversity in a salmon stock.

The loss of older age classes could deprive Brights of some of the ability to withstand environmental adversities. Numerous age classes spawning together combine the genetic variability of several brood years (Helle 1981) and compensate for interannual variability in reproductive success and juvenile-adult survival (Schaffer 1974; Schaffer and Elson 1975). Longevity and multiple ages at reproduction are a functional means whereby chinook salmon retain the benefits of iteroparity (Murphy 1968).

The collapse of the Pacific sardine (*Sardinops caerulea*) is a classic example of the potentially disastrous effects of a diminished number of reproductive age classes under highly variable reproductive success. Reduced from seven or eight reproductive age classes to approximately one by intensive exploitation, the sardine population collapsed when poor environmental conditions caused two successive spawning failures (Murphy 1967). Stock juvenation may have contributed to the collapse of the Spring Creek Hatchery stock of tule fall chinook salmon (Anon. 1986), which underwent a substantial downward shift in age structure (Cleaver 1969; Henry 1971) prior to encountering husbandry problems in the hatchery. As the Bright spawners become concentrated in the younger ages (2-4), they are more vulnerable to recruitment failures, because individual brood years contribute a higher proportion of the spawning population.

A younger age structure causes a shorter generation time, which is not necessarily a threat. The shorter generation time hastens the selection/adaptation process, helping the stock adjust to environmental changes. The rapid and large-scale changes wrought by man probably make genetic responsiveness a useful quality. However, one potential detriment is that over-responsiveness to short-term (perhaps up to a century) changes may leave a stock ill-adapted to former conditions if the changes are ever reversed. Such a scenario might occur if a stock were domesticated, then the hatchery program was terminated.

A variety of spawner sizes may also buffer against environmental variability. The higher fecundities of large fish may make the stock less subject to extinction from overfishing (Weatherley and Gill 1987). Size-related differences in redd site choice and redd construction (van den Berghe and Gross 1984) may help ensure that an entire brood is not destroyed by adverse environmental conditions.

The trend in size and age may reflect intensive selection for those or correlated traits. Strong selection, which can be expected to adversely impact correlated traits (Endler 1986), may cause changes that are not easily measured nor even recognized as the results of selection on a particular trait (Nelson and Soule 1986). As mentioned in the previous chapter, the distinct shift in age at maturity of Spring Creek tules may have been the result of a system of strong age and size selection in the fisheries and hatchery. If so, disease resistance and other adaptive traits may have been unintentionally compromised by the selection. Disease outbreaks were associated with the collapse of the stock (Anon. 1986). If selection by fisheries and other factors is causing the apparent size change in Brights, they might also be causing maladaptive changes in other traits.

In conclusion, substantial costs are associated with declining size in Brights. In addition to having less biomass and being less valuable to the fishery per unit of biomass, small fish probably contribute less to reproducing the stock. The loss of larger and

older life history types may deprive the stock of diversity needed to adapt through evolutionary time.

MANAGEMENT CONSIDERATIONS

In previous chapters I described an apparent decline in average size of Brights, examined several potential causes for the decline, and identified some of the consequences of reduced size and age. This chapter considers how these findings might be useful for improving management of Brights and other stocks of anadromous salmonids.

Holistic Research and Management

The life cycle approach used in this study to examine the potential factors affecting size and age at maturity is particularly useful for management and research. After all, if the abundance and qualities of a salmon population are functions of many interacting environments, how useful is it to focus exclusively on single factors and environments? Rather, would managers not wish to know the net effect of their actions, the ultimate changes in the population after all the counteracting and synergistic forces have been expressed? Addressing fishery management questions in a fragmented rather than holistic manner encourages erroneous or inappropriate conclusions. Riddell (1986) has rightly argued for the holistic approach to understanding the effects of selection on life history traits. However, there are reasons why this approach is rarely attempted.

One major obstacle to a holistic approach is the same problem encountered in this study: we do not know the nature of many of the interactions between environments and management actions and cannot determine the net effects on the resource of a management activity. For example, what are the combined effects of intensively selective fisheries and production-maximizing artificial propagation? Then what happens when oceanographic trends and changes in the freshwater environment (e.g., hydroelectric development) are factored in? Additionally, our knowledge of the ecology and genetics of salmonid populations is miniscule compared to the complexity of those natural systems. We must always be mindful of this fact.

Other drawbacks to a holistic approach to management are inherent in the management systems themselves. There are strong institutional disincentives against changing lucrative and popular current practices such as intensive harvesting and artificial propagation. It can be politically difficult to even investigate, let alone correct, potentially adverse impacts of these practices. Also, fishery management has tended to be compartmentalized into functional areas such as harvest, culture, habitat, and so forth, without the benefit of a higher tier with sufficient vision, purposefulness, and strength to unify and direct the various areas toward defining and achieving long-term resource objectives.

The abundance of jurisdictions that have authority over the fish is also an obstacle to more integrated and responsible management (Fraidenburg and Lincoln 1985). Why should managers of freshwater production attempt to restore or maintain older and larger Brights in the population if the ocean fishers of other states and nations will not allow those fish to escape to spawn? Multiple management jurisdictions with differing goals have been implicated in the economic extinction of at least one important commercial fishery resource, the California sardine (Radovich 1982). Jurisdictions concerned primarily with ocean harvest of Brights have little interest in closely monitoring and reporting, let alone controlling, their impacts on the stock. Therefore our understanding of the net effects of management actions is further obstructed.

The impetus for a more holistic approach must come from within the management organizations. Some are beginning to adopt a "gravel-to-gravel" management perspective that recognizes the importance of all life-cycle environments to stock production and conservation. Perhaps this perspective will promote the holistic scientific investigations that are necessary to synthesize present knowledge and to identify research needs. This is an important step in developing a better base of knowledge regarding complex natural systems.

The challenge still remains, however, to build within management organizations a tier that can institutionally integrate the various fishery management functional areas. Such a level or

activity must be staffed by personnel who possess extraordinarily broad perspectives and knowledge, as well as the management skills to keep various functional factions working toward common objectives. Political support for holistic management could be enhanced by contact between the public and progressive fishery professionals. Personal experience has demonstrated that the general public has a keen interest in learning about salmonid life histories and in protecting salmonid resources. The public and politicians need to know that natural systems are complex, our understanding of them is limited, and "quick fixes" to recognized problems can be destructive in the long term.

Overcoming barriers imposed by the mosaic of jurisdictions may be the greatest challenge of all. The Pacific Salmon Commission (PSC) provides a needed forum for allocating harvests, sharing data, and jointly analyzing options and the results of management decisions (PST 1985). However, the PSC has not been fully effective at achieving conservation objectives (PSC 1988). The efforts of conservation organizations and processes presently being pursued under the Endangered Species Act for some stocks of salmon in the Columbia Basin may contribute to the formulation and enforcement of more stringent conservation practices, even at the international level.

Units for Measuring Resource Value

Several times throughout this paper I challenged the conventional practice of accounting the catch and escapement simply with numbers of fish. Although important and relatively easy to obtain, counts do not fully encompass the value of fish taken in the commercial fisheries and allowed to escape. For example, biomass landed, often with a premium for large fish, is usually the actual basis for value in commercial fisheries. Fecundity, or a more refined measure of fitness, is the real basis for value in the spawning escapement. Harvest allocation schemes based on numbers of fish landed are easily side-stepped with regulations that allow and

even encourage retention of only the largest and most valuable fish. At the same time, adverse trends in sex ratios and average sizes in the escapement could go undetected when only run size is monitored.

Some efforts are being made to better account for ocean harvests. The Analytical Work Group of the Chinook Technical Committee of the PSC adjusts estimates of landed catch to include nonretention mortalities (PSC 1988). This total impact is then expressed in terms of "adult equivalents", i.e., "the potential contribution of fish of a given age to the spawning escapement in the absence of fishing," (PSC 1988, Appendix II, p. 3). Estimated maturity schedules and age-specific natural mortality rates are used to calculate adult equivalents. Such a scheme, which essentially estimates the number of spawners killed by a fishery, credits more adult equivalents to preterminal fisheries taking older fish than to similar fisheries taking the same number of younger fish, hence accounting in part for the age- and size-selectivity in some fisheries. However, because this scheme assumes every fish in the escapement has equal fitness, it still underestimates the impact on stock productivity of fisheries selecting for older and larger fish. These fisheries are more likely to be removing females than males, and among the females they are more likely to be taking the larger (i.e., more fecund) individuals.

Except for the premiums paid for large fish, the value of harvests taken in commercial fisheries is better represented by biomass landed rather than numbers of fish landed. Hence, allocation and accounting based on biomass are more equitable alternatives than present methods. However, allocation and accounting are necessary because the resource is limited; conservation of the stock through adequate escapements is the fundamental concern. Therefore, a superior unit for measuring the impacts of fisheries is fecundity: how is the number of eggs in the escapement reduced by each fishery? Models currently in use to monitor the impacts and regulatory compliance of fisheries can be modified to incorporate sex ratios, sex-specific maturity schedules, and age- or size-specific fecundities for indicator stocks. Granted, fecundity alone does not

incorporate many important characteristics (e.g., sex ratio on the spawning grounds, egg size, genetic and life history diversity) that affect the ability of a stock to reproduce in this generation and to persist through evolutionary time, but it is a great improvement over present methods. Although many agencies have not yet begun to collect age and sex data for escapements (PSC 1988), others have, and their data will provide entree to the next generation of management.

Compared to adult equivalents, accounting for impacts on total fecundity of the escapement would better reveal the impact of size- and age-selective fisheries on the reproductive value of the escapement. Incorporating the necessary estimates of the parameters listed above would certainly compound the complexity and errors of existing accounting models, but the models would be no more likely to be biased in favor of particular user groups or fisheries than at present. Greater effort would have to be invested in obtaining reasonable estimates of the parameters listed above, but having a meaningful and consistent unit for monitoring (potential eggs escaped) would make the greater management investment worthwhile.

My emphasis on number of eggs should not be interpreted as meaning that males are inconsequential, or that fecundity represents the ultimate management unit. I generally assume that selection for males is unlikely in the fisheries and that males would have to compose a small minority of the spawning population before their scarcity would substantially affect the reproductive potential of a stock. Other traits are also important for the longevity of the stock (some of which have already been mentioned), but much must be learned before we can establish and manage for standards for those characteristics.

Van Hyning (1973), Porter et al. (1986), and Weatherley and Gill (1987) also argued for measures that encompass the quality, rather than simply the quantity (i.e., numbers of fish) of the escapement. Total fecundity, or potential eggs escaped, provides a measure of the total quality of the escapement. Other authors go even further, asserting that large egg size and large female size (aside from its direct relationship to fecundity) are also important

components of escapement quality (Hankin and McKelvey 1985; Hankin and Healey 1986). However, the superior fitness of large eggs and the superior spawning ability of large females must be better established before they can be considered important components of escapement quality.

Fishery managers must develop and use tools that are based on more appropriate units of measure than simply numbers of fish.

Harvest Management

Management of the ocean fisheries took a major step forward when estimates of incidental mortalities were incorporated into the chinook model for monitoring fishery impacts (PSC 1988). Care must be taken that these estimates remain current. Although this improvement accounts for fish that are killed but not landed, it does not attempt to determine whether regulatory tactics such as increased minimum size limits in targeted troll fisheries and nonretention in fisheries targeted on other species promote the best use of the resource.

Ricker (1980) is probably justified in attributing reductions in average size and age of the catches in ocean fisheries to harvest regulations. Increasing the minimum size limit for troll-caught chinook salmon in outside waters of British Columbia was contrary to recommendations by Parker and Kirkness (1956) and Funk (1981) that size limits are not compatible with maximum production. However, Ricker (1976), citing Anon. (1970), suggests that the increase in mortalities to sublegal-sized fish that are caught but not retained, which accompanies a higher minimum size limit, may be ameliorated by a reduction in growth overfishing (i.e., catching a cohort of fish too early in life, before they have attained maximum biomass). From computer simulations of ocean troll fisheries on a chinook salmon stock demographically similar to Brights, I found that the net effect of size limit increases on the spawning stock is negative (unpubl. MS). With an increase in minimum size limit and a static quota for numbers of fish landed, value of the catch and numbers of hooking

mortalities increased, but the reproductive value of the escapement (total fecundity) decreased. In this particular exercise, gains in biomass and value landed were not obtained wholly through reductions in growth overfishing, but at least in part from costs to the escapement. Intense harvest of older life history types of chinook salmon caused by minimum size limits is not unlike the selective fishing on subpopulations of pink salmon caused by regulated harvest season openings that consistently occur either early or late in a run (Alexandersdottir and Mathisen 1982). Both may deprive populations of fit and diverse population components.

Unlike troll fisheries, which may kill a minority of nonretained salmon, purse seine fisheries may kill 50% to 90% of the nonretained fish (ADFG and NMFS 1987). Regulations that require thousands of incidentally caught chinook salmon to be discarded in net fisheries targeting on other species (ADFG and NMFS 1987) are clearly wasteful. Further efforts must be made to ensure that ocean harvest regulations are consistent with conservation and allocation objectives.

My findings indicate that the regulations applying to in-river gillnet fisheries should also be reviewed for consistency with conservation objectives. Considering both sexes, the fisheries (particularly in Zone 6) seem to be taking more of the large fish from the run. However, this is based on recoveries of fish reared at Priest Rapids Hatchery and may not apply to the natural component of the run.

The size selectivity of these fisheries merits further study. The likelihood of increased size selection and its consequences should be taken into account when minimum mesh-size restrictions are considered. Managers should not assume that jacks, which pass through the fisheries relatively unscathed, have zero fitness. The persistence of jacks in the Bright runs testifies to the youth of some of the parents, since age at maturity appears to be highly heritable (Konovalov and Ostrovsky 1980; Gjedrem 1983, 1985; Iwamoto et al. 1984; Glebe and Saunders 1986; Ritter et al. 1986; see also Heritability of Size and Age at Maturity, p. 43). It is possible

that proportions of jacks and younger fish in the run are increasing due to the selective action of large-mesh gillnets. To avert this, Ricker (1980) recommends use of gillnets that target on fish considerably smaller than average size. Such a tactic in the Columbia River fall chinook salmon fisheries would be constrained by other conservation concerns (e.g., incidental catch of steelhead) and a desire by fishers to maintain revenues when constrained by ceilings on numbers of fish caught. The latter constraint could be overcome in large part by harvest accounting based on fecundity impacts, since numerous small fish (mostly males) could be caught with smaller mesh sizes without substantially impacting the potential egg deposition of the escapement. Recreational or other fisheries that have greater success on jacks and other small fish may have advantages for managing the average size harvested in a run.

Artificial Propagation

This report has addressed, in more or less detail, three aspects of artificial propagation that deserve reconsideration from fishery managers. Rearing, stock mixing, and mating practices can be improved to ameliorate or avert detrimental changes in life history traits.

Evidence that Brights reared at Priest Rapids Hatchery were younger and smaller than those that reared in the Hanford Reach is consistent with what is known about the effects of rapid growth on maturity. Juveniles that grow well, as in the hatchery environment, tend to mature earlier at smaller average size (although larger at age). Anomalously high proportions of males returning to Priest Rapids Hatchery may also be a response to the rearing environment at the hatchery. The costs to the fisheries and the spawning populations of smaller adults do not seem to be fully appreciated by those who manage hatchery programs.

During the early 1960's, in response to the knowledge that larger smolts had better survival to adulthood, the emphasis at Pacific salmonid hatcheries changed from liberating large numbers of

juveniles to liberating fewer, but much larger, fish (Wahle and Smith 1979). Since then, maximizing survival has become an overriding objective, despite evidence that extreme pursuit of the objective may diminish resource value. Studies with coho salmon by Johnson (1970) and Bilton et al. (1982) showed that maximum value of the resource was obtained with release at sizes that gave less than maximum survival, simply because the smaller fish that did survive matured at larger ages and sizes. The case of excessive returns of spring chinook salmon "minijacks" (mature in the same year they were released as yearlings) to WDF Cowlitz Hatchery provides further impetus against maximizing release size and survival (Paul Peterson, Manager, Cowlitz Hatchery, pers. comm.). Because they are large at release and mature within a few months, minijacks show very high survival to maturity. However, as very small precociously mature males, they have negligible value to fisheries and/or for brood stock. Obviously, high survival of juveniles to maturity cannot be the sole criterion for success of a hatchery program; the quality (e.g., biomass, fecundity) of the returning fish must also be considered.

The same inappropriate measures of hatchery program effectiveness have been applied to Brights. One good example is the yearling-release Snake River Bright program at WDF's Lyons Ferry Hatchery (Seidel et al. undated), in which returning minijacks (nearly 2,000 from the 1983 brood alone) are included in estimates of survival, and no mention is made of the smaller size of all other ages of returning fish. A return rate of 5.2% (fishery contribution and spawning escapement, combined, for 1983 brood yearling on-station releases) is indeed remarkable in the Columbia River Basin above Bonneville Dam, but such rates are misleading when each fish is worth substantially less (due to small size and high male proportions) to the fisheries and to the escapement than a Bright with normal life history and size-at-age. Survival rate alone is an inadequate standard for evaluating hatchery rearing practices. Biomass provided to the fisheries and eggs provided for the escapement are more appropriate bases for evaluation than simply numbers of fish.

It must be noted that early maturity caused by favorable juvenile growth is not likely to directly affect the genetic basis for maturity in a stock. In this case, early maturation is an environment-mediated phenotypic response that would not endure if normal juvenile growth conditions were restored.

Although I found no reason to believe that stock mixing and stock transfers had contributed to reduced size at maturity of Brights, such practices are not necessarily harmless. Mixing of the Bright subgroups probably began with the Grand Coulee Fish-Maintenance Project, which intercepted all chinook salmon spawners passing Rock Island Dam (Rkm 730) and either transplanted them to tributary streams between there and Grand Coulee Dam (Rkm 960; impassable to upstream migrating adults) or used them as brood stock for the artificial propagation part of the project (Fish and Hanavan 1948). The remnants of fall chinook salmon stocks (undoubtedly Brights) that formerly spawned far into the upper Columbia and its tributaries (Fulton 1968) were blended together and relocated, which admittedly may be preferable to complete loss of their genetic resources.

Perhaps more threatening than mixing of the relatively few Brights that migrated over Rock Island Dam is the broodstock trapping that has been occurring lower in the river, where all Bright substocks are co-mingled in the run and are indistinguishable. Although the history of Brights is obscure enough that we cannot be certain that the entire stock or its substocks possess strong genetic adaptations to specific stream environments, differences between the substocks have been described that suggest some genetic distinctiveness (Utter et al. 1982, 1987; Seidel et al. 1988). Even if these differences were not known, it would be imprudent to assume that the stock is genetically homogeneous simply because limited investigations with crude analytical tools have not revealed substantial differences among stock components. Not only does hatchery trapping and transplanting destroy the genetic differences among substocks, it prevents adaptation and genetic stabilization of those units (Becker 1985).

Trapping Bright brood stock at Bonneville Dam for lower river hatchery programs, then transferring the eggs and progeny throughout the basin has been a common practice (e.g., Castoldi and Rasch 1982; Castoldi 1983; Hill 1984; Howell et al. 1985a; Kirby 1985), as have stock transfers between the Snake River and mid-Columbia River substocks (Howell et al. 1985a; Kirby 1985; Abrahamson 1986). Trapping of brood stock at Priest Rapids Dam (for Priest Rapids Hatchery) and at dams on the lower Snake River (for the Snake River egg bank program at Kalama Falls Hatchery and Lyons Ferry Hatchery) also "homogenized" the genomes of upstream substocks, but the impact has probably been less than trapping at Bonneville Dam. To my knowledge, there is no biological rationale for the extensive trapping and transferring that is currently conducted, and it appears that sound stock management is being subordinated to management expediency.

In addition to rearing practices and stock mixing, the broodstock mating regimes at hatcheries require further consideration. Ricker (1980) and Larkin (1981) suggested using hatchery mating regimes that will counteract the selection imposed by fisheries, such as breeding for large size when fisheries tend to depress average size at maturity. However, such a strategy may be short-sighted, given how little is known about correlations among traits and the trade-offs involved with imposing yet another strongly selective force (e.g., selection for large spawner size in the hatcheries) on the stock. Increased susceptibility to disease, lower ocean survival, and other costs may be associated with more intense selection; the collapse of the Spring Creek stock of tule fall chinook salmon (previously described; Anon. 1986) could have been the consequence of intense, selective fisheries and strong hatchery selection in the brood stock. Although hatcheries provide the opportunity to manipulate the traits of a stock through selective mating, they should not be promoted as a quick fix for problems caused by poorly managed fisheries and fish habitat. An undue faith in our primitive understanding of stock genetics is likely to produce

adverse results that may not even be recognizable as consequences of our well intentioned efforts.

For Brights, and as a general rule, I recommend that hatcheries mate spawners in a way that will produce juvenile progeny that resemble juveniles produced by the natural component of the stock (where a natural component exists). Because our knowledge of the composition of the natural population is sparse, a preliminary step is to acquire a better understanding of the fitnesses associated with measurable traits (size is probably the most obvious and commonly measured trait) in natural populations. For example, what are the relative fitnesses of large and small females that spawn in the Hanford Reach? Is mating assortative by size? What proportion of the juvenile population was sired by jacks relative to the proportion of jacks in the spawning population? Genetic marking and other tools are available to begin gathering this information, which would provide guideposts for hatchery mating regimes. Until such information is obtained, any prescription for mating sizes or ages of fish in certain proportions is largely guesswork. Using a small number of jacks for hatchery brood stock, as recommended by Seidel (1983), appears to be a reasonable interim strategy, even though spawning jacks will probably aggravate any problem with depressed size and age caused by hatchery rearing practices.

Role of Stock Abundance

The impact of a human activity on a stock is dependent on what proportion of the stock is affected, which depends on the abundance of the stock and how the level of the activity is managed. For example, consider a terminal fishery that seeks to harvest all of a stock in excess of an escapement threshold (e.g., in-river fisheries on Brights). The lower the abundance of the stock, the smaller the proportion of the stock affected by the fishery. The selectivity of the fishery, or any other activity that impacts a larger proportion of the stock with increasing stock abundance, must be a far greater concern when the stock is abundant, i.e., "healthy". There is

evidence that this occurs in the in-river fisheries for Brights. Ratios of average length (which reflect differences between sizes of fish caught and those escaped) tended to be higher in years when fisheries took higher proportions of the adult run, although the relationship is not statistically significant at 0.05 (simple regression, $P > 0.10$; Fig. 32). When large runs are expected, particular care must be taken that regulations such as gillnet mesh size restrictions minimize size selectivity.

A contrasting situation exists when a set number of fish are impacted regardless of run size. As an example, consider a hatchery program with a static production objective: a certain number of spawners are required to produce a specified number of smolts for mitigation. The lower the abundance of the stock, the greater the proportion of the total stock (hatchery and natural components) that is affected by brood stock selection (as with dam trapping) and hatchery rearing practices. As the run strength of Brights wane and as a greater proportion of the run is propagated artificially, managers of hatchery programs must be aware that their practices will have a greater impact on the quality of the run.

A situation similar to the hatchery example could occur in ceiling-regulated fisheries (such as ocean fisheries managed under the PST) as total abundance of the fished stocks vary and catches do not. The fisheries would exert a greater selective force when exploitation rates are higher, i.e., at lower abundances.

River Development

Despite the obviously major impacts that development of the Columbia River has had on Brights and other stocks of anadromous salmonids (NPPC 1986), it is not clear how average size and age at maturity have been affected. Although fishery managers have played a

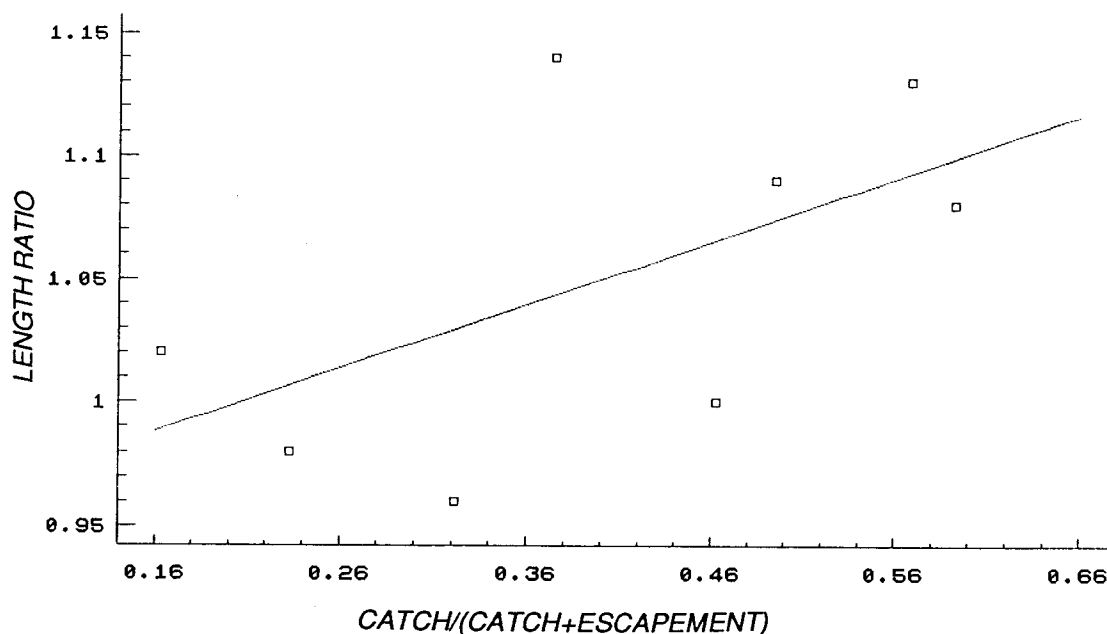


Figure 32. Regression of length ratios on harvest rate in in-river commercial fisheries. Ratios of weighted average fork length for both sexes and all ages in both fisheries (Zones 1-5 and Zone 6), relative to the same lengths in the escapement, were calculated from data in Appendix Table F.2 for years 1980-87. Harvest rates were calculated as Commercial Catch/(Commercial Catch + Escapement) from data in ODFW and WDF (1989), Table 32. Positive slope suggests that higher harvest rates contribute to the intensity of size selection (see text).

relatively minor role in determining the course of the development, there have been, and continue to be opportunities to mitigate the impacts of development. Probably the most important type of opportunity that must be seized is that which improves our own understanding of the biology of the fishes we manage and our appreciation of the consequences of the actions we promote.

Fishery managers often promote measures to increase survival and abundance without acknowledging that there may exist consequences for the quality of the individuals in a stock. Nature is often selective (Endler 1986), and reducing natural mortality may allow genetic frequencies in a stock to shift.

Artificial propagation and providing fishways past natural barriers are two examples of popular management programs that have unrecognized biological costs. Hatcheries generally succeed in reducing the typically high egg-to-smolt mortalities in natural incubating and rearing environments, but what natural selection is foregone in the process? Might smaller females have greater fitness when spawned artificially in a hatchery, with a smaller average size in the run as a result? If so, the losses in average size must be deducted from the more obvious gains in abundance. Reductions in average size are but one change that may be occurring, unnoticed, in hatchery stocks.

As discussed earlier, natural barriers to upstream migration may be major selective forces controlling the characteristics of a stock. Yet, bypassing natural barriers with fishways in order to increase upstream production has been a very popular fishery enhancement practice. W. F. Thompson was one of the earliest advocates of the stock concept, arguing that transplanting anadromous salmonids destined to areas above Grand Coulee Dam would place them in environments to which they were not adapted (Thompson 1951).⁸ Still, when arguing for fishways around Hell's Gate on the Fraser River (Thompson 1945) and Farwell Canyon⁹ (on the Chilcotin River, a Fraser River tributary) to alleviate mortalities to upstream-migrating sockeye salmon, he makes no mention of how such major changes in the migration environment could lead to adaptive changes in the stocks. For example, might the fitness of smaller and more mature individuals be increased sufficiently to cause changes in the average size and degree of maturity at freshwater entry in later generations?

⁸ See also William F. Thompson Papers, Accession No. 2597-3-83-21, Box 8, Subject Series, "Dams". Univ. Wash. Archives, Seattle, WA.

⁹ William F. Thompson Papers, Accession No. 2597-3-83-21, Box 8, Subject Series, "Effect of Farwell Canyon on the Migration of Sockeye Salmon on the Chiloctin (*sic*) River". Univ. Wash. Archives, Seattle, WA.

I am not suggesting that potential effects on size at maturity should be a dominant concern when considering fishery enhancements. However, size at maturity is important and an appropriate trait for consideration here. Nor do I believe that genetic changes due to reduction of natural mortalities are generally adverse, particularly to a degree that would negate the gains in number produced that are expected from such enhancements. However, managers must consider that stocks and their qualities are products of innumerable factors in many environments, and that simple, well intentioned modifications of the environment may have long-term repercussions for stock productivity. When considering ways to mitigate the major damage done to the fishery resources by development of the Columbia River, managers must be mindful that the future health of the resources is highly dependent on stock qualities that are less easy to measure than run size. The simple and conventional mitigative measures for damages caused by river developments (e.g., hatcheries to replace spawning habitat inundated by dam construction; barging smolts around dams and reservoirs) must not be embraced and extolled by fishery managers as good and adequate alternatives to habitat conservation and restoration.

Research Recommendations

During the course of this study it became apparent that many gaps exist in our understanding of the history and biology of Brights. Rather than provide a list of all possible projects that could be conducted to satisfy information needs, I will focus on major points. Also, most of these suggestions do not apply exclusively to Brights.

Historical information is presently an undervalued resource. Care must be taken to preserve and maintain records of research and management activities so that future managers can better understand why the resources are in the condition they are. I found many insights in old records and reports; I also found that much information previously collected could not be located, or was

available only to someone willing to sift through a haystack in hopes of finding a needle that may or may not exist. A Columbia River regional fishery research library is sorely needed and would be a useful repository for records and reports of management and research organizations.

Greater interagency cooperation in managing the fishery resources dictates that data, to the greatest extent possible, be computerized and documented in order to be transferable and useful to other resource managers and researchers. Much of the data now being collected by management agencies is poorly documented; numbers alone are useless unless accompanied by a detailed description of the methods by which the numbers were obtained.

Numerous opportunities to collect basic data are being lost because fishery workers too narrowly define their roles in managing the resource. For example, hatchery personnel who believe they are too busy producing fish to gather basic scientific data on the fish they are spawning and releasing must learn that they are members of a management team that is responsible for far more than producing a specified poundage of juveniles.

A certain amount of research effort must continue to be invested in reviews and syntheses. Studies that mine historical information can produce gems of insight for current work. As knowledge expands and research becomes more highly specialized, someone must tie together the information generated by the radiating disciplines and illuminate gaps in the information base. Fishery science must not be allowed to become an assortment of disjoint disciplines. Life history theory provides a valuable framework on which to build our understanding of the biology of salmon populations.

So little is known about the complex life histories and ecology of Brights and other anadromous salmonids that almost any well designed and well conducted study into these aspects should produce useful results. In the freshwater part of the life cycle, investigations into the fitnesses of various phenotypes (e.g., large or small individuals) for spawning, incubation, and rearing in

different environments are needed. Findings of such studies would be useful in understanding the significance of size at maturity, particular spawning microhabitat types, hatchery mating practices, and size-selective fisheries for the viability of stocks. The influence of the maternal phenotype is one factor in this segment of the life cycle that has received too little scientific attention relative to its probable importance (see *Maternal Influences*, p. 50). Although she dies soon after spawning, the maternal phenotype continues to exert a strong influence over the viability of her progeny. This link across generations from maternal mating to juvenile rearing must play an essential, but little-understood role in the evolution and production of a stock.

The estuary and ocean environments are likewise poorly understood relative to the important roles they play in the welfare of stocks such as Brights. The Columbia River estuary is greatly influenced by human activities, yet we really have no idea how those activities impact the quality of this important rearing environment. The relationship between mega- and mesoscale climatic and oceanographic phenomena and the growth and survival of Brights warrants further investigation. For example, how are local and regional trends in ocean temperature reflected in the survival of young Brights emigrating from the Columbia River and in the growth of those fish in northern rearing areas? Such information has much practical value for predicting run strengths and interpreting changes in average size and age at maturity. Studies in Pearcy (1984) and the work of Cushing (1981, 1982), Mysak et al. (1982), and Hollowed et al. (1987) exemplify productive inquiries in this area. Fishery scientists living in their terrestrial, two-dimensional worlds must seek to understand the atmospheric and oceanographic processes and phenomena that determine the marine environments of salmon stocks.

The genetic processes of salmon populations, particularly natural stocks, are poorly understood and worthy of additional scientific effort. Not only is it important to describe differences between substocks so that between-deme genetic diversity can be appropriately managed and conserved, but it is also necessary to

further define the implications of tetraploidy, sex-related inheritance, and other little-understood genetic conditions and processes. Principles of agricultural genetics must be further scrutinized to determine how they should and should not be applied to salmonid culture. For example, how prudent is size selection during hatchery spawning when we do not know what fitness-related traits may be negatively correlated with spawner size?

Research into the effects of harvests on stock demographics must continue. The measurement of incidental mortalities in ocean fisheries appears to be of ongoing importance and is relatively simple to accomplish. Political and social obstacles may be the greatest impediment to such research on fishery impacts. Statistical tools are needed to interpret recovery patterns of CWTs. Concentrated effort on monitoring some key index stocks, such as Brights, may reveal important aspects of their distribution, growth, vulnerability to fishing, and natural mortality rates that are not presently known. In-river, the trends in size-related run timing should be monitored, and the size selectivity of various gillnet mesh sizes should be studied in more detail. Development of new and existing computer models, together with acceptance of more appropriate units for measuring resource value, will permit a better evaluation of management options and accounting of fishery impacts.

SUMMARY CONCLUSIONS

1. THEORETICAL CONTEXT

- 1.1. Life history traits, such as size and age at maturity, are expressions of the environments through which Brights pass during their development.
- 1.2. Developmental environments influence size and age at maturity in at least four principal ways: (1) directly selecting for particular trait values; (2) selecting on traits correlated with size and age at maturity; (3) inducing purely phenotypic responses, which do not change the relative fitnesses of size and age genotypes; and (4) promoting random genetic events by reducing effective population size.
- 1.3. It is reasonable and prudent to assume that prevailing trait values (e.g., modal sizes and ages at maturity) are to some degree adaptive for the sequence of environments encountered by Brights during their life cycle and that a range of trait values are necessary for the stock to adapt to environmental changes.

2. WHAT IS A BRIGHT?

- 2.1. Salmonids compose a diverse and highly adaptable family.
- 2.2. Like other anadromous salmonids of the Columbia River, Brights have been subjected to excessive harvesting, extensive habitat destruction and modification, and artificial propagation. The sizeable runs of Brights in recent years attest to the stock's adaptability to major anthropogenic environmental changes.
- 2.3. Brights, although managed as a single stock, are a heterogeneous assemblage of natural and hatchery production units covering a broad geographic area.
- 2.4. Brights were probably first recognized as a distinct race of fall chinook salmon when investigations on the Celilo Falls Indian dipnet fishery began in the 1940's.

- 2.5. There is some question as to whether Brights existed as a distinct group prior to the 1930's. It is quite possible that the stock emerged within the last century from late-run summer fish that were protected by the traditional fall season fishing closure. Habitat fragmentation, underseeded rearing areas, and many other environmental changes could have facilitated the development of the stock.
- 2.6. Data on fall-season fish weights collected below Celilo Falls before the advent of coded wire tagging cannot be accepted, without qualification, as representative of Brights.
- 2.7. This study focussed on the Brights that spawn naturally in the Hanford Reach and those propagated at Priest Rapids Hatchery. These two units account for the majority of Bright production.

3. CHANGES IN BRIGHT SIZE AND AGE AT MATURITY

- 3.1. The best historical weight data available on Brights suggest a decrease in average weight of Brights of approximately 2.7 kg since the 1910s. At $0.1 \text{ lb}\cdot\text{yr}^{-1}$, the rate of decrease in average weight is about one-third and one-half the rates estimated for declines in average weight of chinook caught in ocean fisheries of, respectively, British Columbia and Southeast Alaska (Ricker 1980, 1981).
- 3.2. The data were inadequate to estimate a trend in average age.

4. CAUSES OF SIZE AND AGE CHANGES

4.1. Introduction

- 4.1.1. Two models are helpful in conceiving how average size and age at maturity are determined. The Causal Sphere model captures the complex array of factors and their interactions that influence size

and age at maturity. A mathematical model provides a mechanism for explicitly describing factors that contribute to changes in the traits, but there is rarely sufficient data to develop such a model.

4.1.2. Size and age at maturity are closely related heritable quantitative traits, and they may be subject to sex-related inheritance.

4.2. Early Rearing

4.2.1. In Brights, maternal parents have the potential, depending on their size, to influence the viability of their offspring through time of spawning, choice of spawning site, and egg size. Such maternal influences, which may be sensitive to changing environments, can generate changes in average size and age of the stock in subsequent generations.

4.2.2. Juvenile growth conditions can influence the age at maturity of individual fish, particularly those genetically predisposed to mature at a young age.

4.2.3. Much evidence indicates that larger juveniles have better survival, which suggests that rapid growth confers survival advantages.

4.2.4. Too little is known about the natural incubation and rearing ecology of Brights to determine if the major environmental changes in the Hanford Reach since the 1940s have contributed to the apparent decline in average size of mature fish.

4.2.5. In 1980-87, spawners that had been reared at Priest Rapids Hatchery were smaller, younger, and more likely to be male than the Brights spawning naturally in the Hanford Reach and sampled during spawning ground surveys. Favorable growth conditions at Priest Rapids Hatchery and an emphasis on releasing large juveniles are probably responsible in part for the differences.

4.3. Outmigration

4.3.1. I could not determine whether or how the high mortalities caused by downstream passage through the mainstem dams and reservoirs may be selective for size and age at maturity.

4.3.2. Conditions in the Columbia River estuary are most likely to influence adult size and age through juvenile growth rates. It is not known how changes in the estuary environment may have influenced trends in average size and age of Brights.

4.4. Ocean

4.4.1. Growth conditions for Brights in the ocean are probably dependent on large-scale climatic and oceanographic processes that govern primary production in the Northeast Gulf of Alaska.

4.4.2. Because the trend in average size of Brights is contrary to what would be expected from trends in physical and biological conditions in the marine environment, I conclude that changes in ocean growth conditions did not contribute to the decline in size.

4.4.3. I do not know whether natural ocean mortality rates have changed in a way that would contribute to a decline in average age, and hence average size.

4.4.4. The ocean fisheries of Southeast Alaska and British Columbia appear to select against large size and old age in Brights. Whether the selection by those fisheries has intensified or whether decades of selection has produced a long continual genetic response toward smaller size and younger age is not known.

4.5. Spawning Migration

- 4.5.1. There were trends toward later dates of mean passage for both jack and adult fall chinook salmon (probably mostly Brights) at The Dalles Dam between 1962 and 1987, with jacks showing a greater rate of change. Whereas the mean date of passage for jacks preceded that of adults in the run prior to 1971, the order was reversed thereafter. There is no evidence that this size-related run timing has promoted size selectivity in the in-river gillnet fisheries.
- 4.5.2. Generally, I found no evidence that larger fish or more females were caught when 8-in. minimum gillnet mesh size restrictions were in effect. However, many fishers use 8-in. mesh even when it is not required.
- 4.5.3. Using recovery data from coded wire tagged fish originating from Priest Rapids Hatchery, I found that the in-river fisheries usually took larger fish and a higher proportion of females than were found in the escapement. The in-river fisheries appear to be selecting for smaller size (by removing the larger fish), at least in the Priest Rapids Hatchery component of the run.
- 4.5.4. The in-river fisheries caught larger Priest Rapids Hatchery males and smaller Priest Rapids Hatchery females than were found in the escapement. The fisheries appear to be selecting differently for size in the two sexes, which could be meaningful under sex-related inheritance.
- 4.5.5. If natural Brights from the Hanford Reach are indeed larger than Priest Rapids Hatchery Brights, the fisheries would be less likely to select larger natural fish than escaped.

- 4.5.6. Evidence for size selection in the fisheries applies only to years since 1978. It is likely that the in-river fisheries during earlier decades, when much of the apparent size decline occurred, also targeted larger fall chinook salmon.
- 4.5.7. It is possible that natural barriers such as Celilo Falls selected for large size in Brights and that fishways, which appear to be easily passable to salmon of all sizes, have given small Brights greater fitness. However, sections of Celilo Falls were easily passable to upstream migrants, and we have no way of knowing how the fish of various sizes chose their routes or fared in their attempts to pass the barrier.

4.6. Spawning

- 4.6.1. Female Brights spawning naturally in the Hanford Reach are known to place their redds at great depth where water velocities are high and substrate particle sizes are large. The reason for such siting is not known, although deep spawning may have been adaptive in former times, and eggs incubating in large gravels may have survival advantages. Large female size is probably adaptive for spawning under such conditions.
- 4.6.2. Sexual selection may favor large males, but the overall relative fitness of small males, which may "sneak" fertilizations, is not known.
- 4.6.3. It is not known whether the extensive changes in the natural spawning environment of Brights have contributed to declining size at maturity by improving the fitness of small spawners.
- 4.6.4. Without knowing more about size selection during natural spawning, it is not possible to determine whether spawning practices and incubation at Priest

Rapids Hatchery select differently, relative to the natural environment, for adult size. It does not appear likely that mating practices at the hatchery have contributed to a decline in average size.

4.7. Causes: A Concluding Discussion

- 4.7.1. The argument that fisheries account for too small a fraction of total lifetime mortalities to be a major selective force for genetic changes in size and age at maturity is refuted. A fishery, or any other source of mortality, impacts a stock according to the proportion of the stock taken and the selectivity toward the trait of interest, assuming that all individuals alive at the time have equal fitness.
- 4.7.2. The perseverance of larger and older phenotypes in the presence of seemingly intensive and long-term selection against those attributes by fisheries suggests the presence of countervailing selection at some point in the Bright life cycle -- possibly during spawning, incubation, or early rearing.
- 4.7.3. Countervailing selection may resist changes in average values of important life history attributes, but that resistance may well reduce productivity in the stock.
- 4.7.4. Given the apparent heritability of size and age at maturity and the apparent selectivity of many of the factors discussed, it is likely that a decline in size of Brights reflects, in part, genetic changes.
- 4.7.5. I was able to describe in only a coarse way the more apparent factors and their interactions that may influence size and age at maturity in Brights.

5. CONSEQUENCES OF CHANGES IN SIZE AND AGE

- 5.1. Reduced average size in Brights means lower commercial value, because of reduced biomass (for a given number of fish) and lower unit prices for smaller fish. Smaller fish also have lower value for other uses, consumptive and nonconsumptive.
- 5.2. A trend toward smaller average size may reduce productivity of the stock. Larger females are more fecund, and other fitness advantages may be associated with large size.
- 5.3. The loss of larger and older life history types may reduce the adaptive capacity of the stock, making it more vulnerable to environmental variations.

6. MANAGEMENT CONSIDERATIONS

- 6.1. Despite drawbacks, a holistic approach to researching and managing anadromous salmonid resources is superior to focusing narrowly on single environments and factors. Institutional changes are needed to facilitate this approach.
- 6.2. Accounting for catches and escapements in terms of numbers of fish is inadequate. Because conservation is the critical long-term objective of fishery management, I propose using the impacts on total fecundity in the escapement as a more reasonable basis for evaluating fisheries and other management activities.
- 6.3. Regulating ocean harvests with minimum size limits and other forms of nonretention is almost certainly contrary to good resource conservation objectives.
- 6.4. The size-selectivity imposed on Brights by minimum mesh size restrictions should be more thoroughly evaluated so that possible adverse impacts of such regulations can be better defined.
- 6.5. Evaluating hatchery programs solely on the basis of smolt-to-adult survival is inappropriate. Measuring hatchery

- production by biomass contributed to the fisheries and eggs contributed to the escapement incorporates more of the values that artificial propagation seeks to maximize.
- 6.6. I condemn the routine practices of trapping hatchery brood stock at dams, particularly at points where many stock components are co-mingled, and transplanting throughout the basin. Such practices destroy linkages among co-adaptive gene complexes and prevent adaptation to particular home-stream environments.
- 6.7. I make the general recommendation that hatcheries such as Priest Rapids use mating schemes that produce progeny resembling those in the natural component of the run, although little is presently known about the genotypes or phenotypes (related to size and age at maturity) that prevail among juvenile Brights in the Hanford Reach.
- 6.8. Size and age selection caused by various management activities can be greater or less, depending on stock abundance and how the activities are managed. Care must be taken in the in-river fisheries (regulated for target escapement) when stock abundance (hence harvest rate) is relatively high. Conversely, hatchery practices and ceilinged fisheries can have a greater selective impact when stock abundance is relatively low.
- 6.9. With regard to river developments, fishery managers must beware that they do not underestimate the complexity of the natural systems they manage, nor overestimate their own abilities to mitigate for harmful developments or to enhance depleted runs.
- 6.10. To facilitate future research, historical information must be preserved and kept available. Data now being collected must be fully documented and, to the greatest extent possible, computerized so that it is readily understandable to, and accessible by other researchers and managers. Additional studies are needed most in the spawning, incubation, and early rearing ecology of

Brights; the influence of the ocean environment on survival and growth; the genetic processes of salmonid populations; and the effects of harvest tactics on stock demographics. Emphasis must also be placed on work that integrates historical information with present conditions and on work that synthesizes the knowledge being obtained in the radiating subdisciplines of fishery science.

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APPENDICES

APPENDIX A

Historical Data of Bright Average Size

(References for sources cited in this appendix are listed at the end of the appendix.)

Table A.1. Data used to determine trend in Bright average weight.

Fig. 8			Mean		Dates	
Code	Source	Description	Year	Weight (lb)	n	Sampled
a	Chapman (1940)	Mean weights of trap-caught fish purchased by McGowan & Sons, Ilwaco, WA. Gillnet-caught fish were larger.	1918	24.3	4,333	August
			1919	22.0	2,853	August
			1920	25.4	5,101	August
			1921	26.8	4,739	August
			1922	26.4	5,838	August
			1923	15.5	232	August
			1924	19.1	1,861	August
			1925	27.2	8,076	August
			1931	17.8	5,225	August
			1932	24.3	8,145	August
			1933	23.1	5,620	August
			1934	23.4	2,739	August
			b	Rich (1940a)	Celilo Falls catch by unknown gear (presumed by Rich to be mostly dipnet-caught). Substantially lower (4-7 lb) average weights at Celilo relative to lower river gillnet catch in same season suspected to be result of removal of large fish by downstream gillnets.	1939

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Table A.1. (continued)

Fig. 8		Description	Year	Mean Weight		Dates Sampled
Code	Source			(lb)	n	
c	Schoning et al. (1951)	Random weights of dipnet-caught fish at Seufert Bros. Cannery, The Dalles, OR (probably caught at Celilo Falls). Seine-caught fish from same time just below Celilo Falls averaged 2.6 lb smaller.	1949	18.0	235	9/14-9/16
d	USFWS (1953, 1954)	Celilo Falls dipnet-caught adults and jacks. Closed commercial period not sampled because fishers commonly did not retain smallest fish.	1952	18.2	5,691	8/14-26 & 9/10-12/31
			1953	22.3	459	8/13-26 & 9/10-12/31
e	WDF (1954-58)	Celilo Falls dip bag net daily landings (from commercial fish tickets).	1954	22.4	11,370	8/26-9/29
			1955	17.8	8,774	8/16-11/2
			1956	21.2	6,399	8/1-9/13
f	WDF (1980-86)	Commercial setnet and gillnet daily landings in The Dalles and John Day pools (fish tickets).	1980	19.0	1,340	9/3-9/11
			1981	18.2	1,084	9/1-10/2
			1982	16.2	232	9/2-9/3
			1983	16.0	3,434	8/31-10/7
			1984	16.2	4,071	8/7-10/15
			1985	18.2	11,714	8/25-9/28
			1986	18.2	22,970	8/19-10/4

Table A.2. Historical data that was not used in estimating the trend in average size of Brights.

Source	Year(s)	Description	Reason(s) Data Not Used
Chapman (1940)	1926-30 1935-39	Mean weights of combined gillnet-caught and trap-caught fish purchased during August by McGowan & Sons, Ilwaco, WA.	1) Probably high proportion of gillnet-caught fish. 2) Average weights biased high due to gillnet selectivity. 3) Mixed fall chinook stocks. 4) Makes trend more conservative.
Pulford (1964)	1952-56	Zone 6 commercial gillnet catch sampled at processors during late fall season (15 Sept. to Nov.)	1) Assume gillnet catch biased toward large. 2) Average weights anomalously low, highly variable, contradictory of better samples. 3) Makes trend more conservative.
WDF (1954-58)	1957-58	Ostensibly Celilo Falls dip bag net daily landings from commercial fish tickets during Sept.-Oct.	Celilo Falls flooded in these years; actual source of the sampled fish is unknown.
WDF (1959-61)	1959-61	Ostensibly The Dalles Dam Indian dip bag net daily landings from commercial fish tickets during fall season.	Fishing was not allowed at the dam; actual source of the sampled fish is unknown.

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Table A.2. (continued)

Source	Year(s)	Description	Reason(s) Data Not Used
WDF (1963-64, 1966-86)	1963-64 1966-86	Klickitat County (WA) Indian set net daily landings from commercial fish tickets.	Probably high proportion of Bonneville Pool Hatchery tule fall chinook.
Chambers (1960) Meekin et al. (1971) Bauersfeld (1978)	1959 1961-67 1977	Lengths of Bright spawners at McNary spawning channel, at Rocky Reach spawning channel, and in the Hanford Reach, respectively. Weights can be estimated from functional regressions (Ricker 1975) of weight on length derived from fishery samples taken in later years.	Calculated weights considered inferior to weight data for similar years from other sources.
Gunsolus and Wendler (1972)	1938-1951	Total pounds and estimated total numbers of chinook taken during fall season in Zone 6 commercial fishery from fish tickets. Average weight can be calculated.	An average weight of 20 lb/fish was assumed for estimating number of fish from reported weights of lots in these data.

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Table A.2. (continued)

Source	Year(s)	Description	Reason(s) Data Not Used
Gunsolus and Wendler (1972)	1952-71	Total pounds and estimated total numbers of chinook taken during fall season in Zone 6 commercial fishery (mostly gillnet). Pounds are from Oregon and Washington fish tickets; weights are calculated based on weekly average weights from agency bio-sampling of the catch.	1) Includes unknown and possibly high proportion of Bonneville Pool Hatchery tules. 2) Based on data from later years (ODFW and WDF 1988), average weights of tules and Brights differ (tules generally larger). 3) Calculated average weights from Zone 6 fall chinook (from data in ODFW and WDF, 1988) are not correlated with estimated proportion of Brights in the catch.
ODFW and WDF (1988)	1960-87	(Same as for Gunsolus and Wendler, 1972, above)	(Same as for Gunsolus and Wendler, 1972, above)
Schoning et al. (1951)	1949	Random weights of fish caught by seine and by mixed gears and purchased by Seufert Bros. Cannery, The Dalles, OR, in mid-Sept.	1) Less comparable to data of other years than dipnet-caught sample weight provided by same source. 2) Seine-caught fish had smaller average size than dipnet-caught fish.

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Table A.2. (continued)

Source	Year(s)	Description	Reason(s) Data Not Used
Catch records of the F. M. Warren Packing Co., The Cascades. Oregon Historical Society MSS 1141-2, Portland, OR.	As early as 1909	Numbers and pounds of daily catches by species for each company fishwheel, mostly in the area of The Cascades.	1) Too few chinook caught in August (wheels inoperable at low flows) to calculate meaningful average weights. 2) Small fall catch probably included tules.
Catch and purchase records of Seufert Bros. Cannery, The Dalles, OR. Oregon Historical Society MSS 1102, Portland, OR.	1885-1950s	<u>Pounds</u> caught/purchased by species and day, including fall chinook caught by Indian fishers at Celilo Falls.	Numbers of fish were not recorded, hence average weights could not be calculated.

APPENDIX A REFERENCES

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1954. Summary report on Indian fishery census, Celilo Falls and vicinity, 1953. Portland, OR. 29 p. + maps. [copies available from R. Beaty, Columbia River Inter-Tribal Fish Commission, 729 NE Oregon, Suite 200, Portland, OR, 97232]

WDF (Washington Department of Fisheries). 1954-86. (Annual commercial fish harvest data published under various titles): Columbia River salmon, fish and shellfish (1954); Columbia River salmon (1955); Puget Sound, Gray's and Willapa Harbor, Columbia River salmon (1956); Columbia River salmon and other fish (1957), Columbia River salmon, fish and shellfish (1958-64, 1966-70, 1973-74); Columbia River salmon, bottomfish and shellfish (1971-72); Puget Sound, Gray's Harbor, Willapa Harbor, and Columbia River salmon (1975); Washington salmon landings (1976-86). Olympia, WA. (Also available at Washington Department of Fisheries, Columbia River Laboratory, Battle Ground, WA.)

APPENDIX B

Measures and Definitions for Selection of
Quantitative Genetic Traits

(References for cited sources are listed with those from the text, p. 191.)

Directional selection of a quantitative genetic trait occurs when the mean value of the trait differs between the breeding individuals and the population as a whole. The degree of directional selection can be expressed as the selection differential, S :

$$S = \bar{X}' - \bar{X}$$

where \bar{X}' and \bar{X} are, respectively, the mean trait values of the breeding individuals and the population as a whole (Appendix Fig. B.1). (Formulas and definitions are adapted from Falconer 1981.) For analyses in this study, the mean lengths of the run (prior to removals by the fishery) are subtracted from the mean lengths of escaping spawners to estimate the degree of selection by the fishery on mean length in the spawning population. Selection differential must not be confused with the difference between means of individuals removed by the fishery and the population before or after removal.

Another measure -- selection intensity, i -- standardizes the selection differential by the standard deviation of the phenotypic trait (σ_p),

$$i = \frac{S}{\sigma_p}$$

to reflect the degree of selection relative to natural variability of the trait. Selection intensity, which is qualitatively similar to the selection differential, was not used in this study.

The heritability of a trait, h^2 , is calculated by comparing the response to selection (R , the change in the trait means from the entire parent population to progeny of the selected breeders) to the selection differential:

$$h^2 = \frac{R}{S}$$

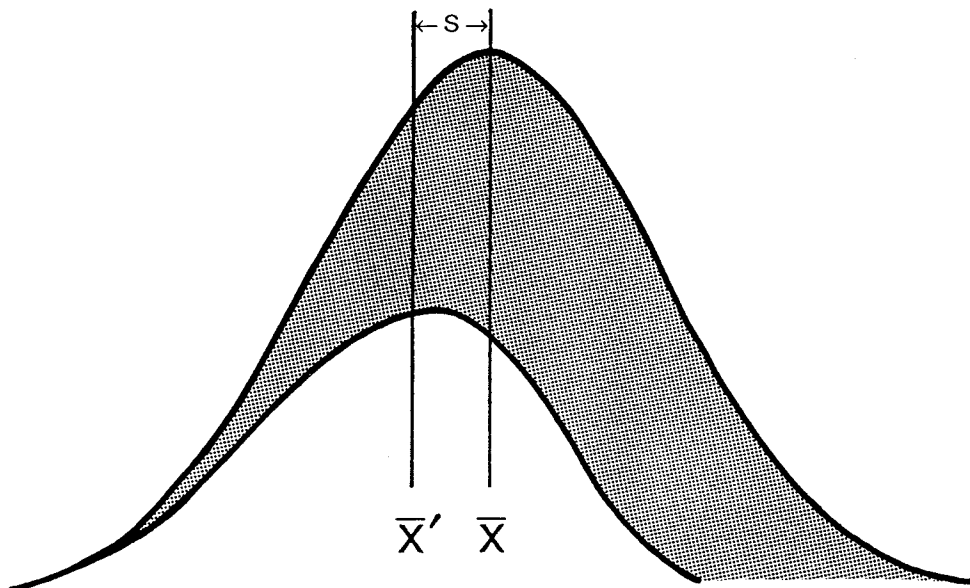


Figure B.1. Selection differential (S): the difference in mean lengths of Bright spawners before (large curve) and after (smaller curve) selective removal of the largest individuals (shaded area).

This is the method used by selective breeding studies cited in this report for determining heritability of age at maturity in chinook salmon. Heritability was not calculated in this study.

APPENDIX C

Coded Wire Tag Codes Used in Analyses

(Reference for cited source is listed with those from the text, p. 191.)

Table C.1. Coded wire tag (CWT) codes used to identify Brights for analyses in this study. Subyearling chinook outmigrants collected at McNary Dam were tagged for a National Marine Fisheries Service transport evaluation study, with control lots released in the McNary Dam tailrace and experimental lots trucked or barged for release below Bonneville Dam. Priest Rapids Hatchery code groups are subyearling and yearling (code 632330, only) Brights, sometimes of mixed substock parentage. See PMFC (1988) for additional release data for the code lots.

<u>Collected at McNary Dam</u>			<u>Priest Rapids Hatchery</u>		
Code	Brood Year	Analyses ^a	Code	Brood Year	Analyses ^a
031730	1980	G	131101	1975	H A L F
031731	1980	G	131202	1975	H A L F
031732	1980	G	631662	1976	H A L F
031733	1980	G	631741	1977	H A L F
031736	1980	G	631821	1978	F
231609	1981	G	631948	1979	H A L F
231610	1981	G	631958	1978	H
231611	1981	G	632017	1978	F
231612	1981	G	632155	1980	H A L F G
231613	1981	G	632252	1981	F G
231614	1981	G	632261	1980	F G
231615	1981	G	632330	1984	F G
231623	1982	G	632456	1981	H L F G
231624	1982	G	632611	1982	H L F G
231625	1982	G	632612	1982	H L F G
231626	1982	G	632848	1983	H L F G
231627	1982	G	632859	1983	H L F G
231628	1982	G	633221	1984	H L F G
231629	1982	G	633222	1984	H L F G
231630	1982	G	632860	1983	H L F G
231631	1982	G			
231632	1982	G			
231633	1982	G			

^a Analysis codes:

H For representing hatchery fish in comparison with naturally produced fish in Priest Rapids Hatchery Environment, p. 70.

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Table C.1. (continued)

(Analysis codes -- continued):

- A For evaluating mean age of ocean and in-river commercial catches with the escapement in Ocean Fishing, p. 97.
- L For comparing mean length-at-age in ocean and in-river fisheries with the escapement in Ocean Fishing, p. 97.
- F For determining size-selectivity of in-river fisheries in In-river Fisheries, p. 110.
- G For evaluating the selectivity of in-river commercial gillnet fisheries under minimum mesh size restrictions in In-river Fisheries, p. 110.

APPENDIX D

Data for Comparing Hatchery and Natural Bright Spawners:
Length, Age, and Sex Composition

Table D.1. Mean lengths and ages of hatchery and natural Bright spawners, males, all ages. All ratios are computed as hatchery mean divided by natural; hence, ratios less than 1.0 indicate the hatchery mean is the lesser. Hatchery spawners (Type = Hat.) were produced and coded wire tagged (see Appendix C) at Priest Rapids Hatchery. Brights spawning in the Hanford Reach are presumed, with some exceptions (see text), to have been produced naturally (Type = Nat.). Only records containing a length between 300 mm and 1500 mm and an age were used. Overall values are based on the unweighted of annual mean lengths for all 8 yr.

Return Year	Type	n	Length			Age		
			Mean (mm)	SD	Ratio	Mean (yr)	SD	Ratio
1980	Hat.	68	824	175.2	.97	4.03	0.92	1.04
	Nat.	584	853	201.6		3.88	0.94	
1981	Hat.	61	668	204.4	.85	3.16	1.03	.91
	Nat.	407	789	218.7		3.47	0.96	
1982	Hat.	57	723	161.4	1.00	3.07	0.70	.98
	Nat.	1090	726	192.6		3.15	0.86	
1983	Hat.	60	739	168.4	.97	3.37	0.55	.99
	Nat.	1403	762	193.8		3.41	0.75	
1984	Hat.	162	672	179.8	.94	3.05	0.77	.93
	Nat.	1738	714	228.3		3.28	0.96	
1985	Hat.	644	645	149.8	.92	2.89	0.78	.92
	Nat.	442	700	229.9		3.16	1.03	
1986	Hat.	401	618	190.8	.92	2.78	0.86	.91
	Nat.	698	675	223.0		3.07	0.91	
1987	Hat.	252	711	151.0	.93	3.33	0.57	.96
	Nat.	610	763	206.9		3.46	0.84	
OVERALL	Hat.	8	700	64.5	.94	3.21	0.39	.96
	Nat.	8	748	56.6		3.36	0.26	

Table D.2. Mean lengths and ages of hatchery and natural Bright spawners, females, all ages. All ratios are computed as hatchery mean divided by natural; hence, ratios less than 1.0 indicate the hatchery mean is the lesser. Hatchery spawners (Type = Hat.) were produced and coded wire tagged (see Appendix C) at Priest Rapids Hatchery. Brights spawning in the Hanford Reach are presumed, with some exceptions (see text), to have been produced naturally (Type = Nat.). Only records containing a length between 300 mm and 1500 mm and an age were used. Overall values are based on the unweighted of annual mean lengths for all 8 yr.

Return Year	Type	n	Length			Age		
			Mean (mm)	Sample SD	Ratio	Mean (yr)	Sample SD	Ratio
1980	Hat.	106	919	91.5	1.01	4.79	0.47	1.05
	Nat.	971	912	76.0		4.57	0.60	
1981	Hat.	65	877	79.9	1.00	4.2000	0.59	1.00
	Nat.	847	881	68.2		4.1995	0.48	
1982	Hat.	45	804	92.0	.91	3.60	0.68	.85
	Nat.	1055	882	87.6		4.24	0.61	
1983	Hat.	36	868	53.8	1.00	3.94	0.23	.98
	Nat.	1271	866	72.6		4.02	0.39	
1984	Hat.	75	838	78.1	.97	3.93	0.47	.96
	Nat.	1257	867	121.1		4.08	0.64	
1985	Hat.	154	829	86.7	.92	3.92	0.68	.92
	Nat.	315	904	80.7		4.29	0.56	
1986	Hat.	258	859	68.7	.97	4.00	0.48	.94
	Nat.	538	889	79.4		4.24	0.54	
1987	Hat.	184	868	96.0	.96	4.05	0.69	.95
	Nat.	494	902	81.4		4.27	0.57	
OVERALL	Hat.	8	858	34.7	.97	4.05	0.34	.96
	Nat.	8	888	17.1		4.24	0.16	

Table D.3. Mean lengths and ages of hatchery and natural Bright spawners, males, ages 3-6. All ratios are computed as hatchery mean divided by natural; hence, ratios less than 1.0 indicate the hatchery mean is the lesser. Hatchery spawners (Type = Hat.) were produced and coded wire tagged (see Appendix C) at Priest Rapids Hatchery. Brights spawning in the Hanford Reach are presumed, with some exceptions (see text), to have been produced naturally (Type = Nat.). Only records containing a length between 300 mm and 1500 mm and an age were used. Overall values are based on the unweighted of annual mean lengths for all 8 yr.

Return Year	Type	n	Length			Age		
			Mean (mm)	SD	Ratio	Mean (yr)	SD	Ratio
1980	Hat.	66	836	161.8	.96	4.09	0.87	1.03
	Nat.	556	874	183.6		3.97	0.87	
1981	Hat.	39	785	158.6	.89	3.82	0.67	.98
	Nat.	318	878	155.4		3.89	0.63	
1982	Hat.	47	782	106.0	.98	3.30	0.54	.94
	Nat.	835	798	157.9		3.50	0.67	
1983	Hat.	58	749	161.8	.93	3.41	0.49	.95
	Nat.	1249	803	163.9		3.59	0.59	
1984	Hat.	121	756	123.4	.92	3.40	0.54	.91
	Nat.	1268	821	166.6		3.76	0.66	
1985	Hat.	444	719	120.1	.88	3.30	0.60	.89
	Nat.	299	819	182.7		3.71	0.80	
1986	Hat.	209	773	123.5	.98	3.50	0.59	.98
	Nat.	477	792	167.4		3.57	0.66	
1987	Hat.	252	711	151.0	.89	3.33	0.57	.92
	Nat.	552	797	187.8		3.61	0.72	
OVERALL	Hat.	8	764	39.9	.93	3.52	0.29	.95
	Nat.	8	823	34.4		3.70	0.16	

Table D.4. Mean lengths and ages of hatchery and natural Bright spawners, females, ages 3-6. All ratios are computed as hatchery mean divided by natural; hence, ratios less than 1.0 indicate the hatchery mean is the lesser. Hatchery spawners (Type = Hat.) were produced and coded wire tagged (see Appendix C) at Priest Rapids Hatchery. Brights spawning in the Hanford Reach are presumed, with some exceptions (see text), to have been produced naturally (Type = Nat.). Only records containing a length between 300 mm and 1500 mm and an age were used. Overall values are based on the unweighted of annual mean lengths for all 8 yr.

Return Year	Type	n	Length			Age		
			Mean (mm)	SD	Ratio	Mean (yr)	SD	Ratio
1980	Hat.	106	919	91.5	1.01	4.79	0.47	1.05
	Nat.	970	912	76.0		4.58	0.59	
1981	Hat.	65	877	79.9	.99	4.2000	0.59	1.00
	Nat.	845	882	65.6		4.1995	0.47	
1982	Hat.	45	804	92.0	.91	3.60	0.68	.85
	Nat.	1055	882	87.6		4.24	0.61	
1983	Hat.	36	868	53.8	1.00	3.94	0.23	.98
	Nat.	1269	866	71.5		4.02	0.38	
1984	Hat.	75	838	78.1	.95	3.93	0.47	.95
	Nat.	1213	883	87.4		4.16	0.51	
1985	Hat.	154	829	86.7	.92	3.92	0.68	.92
	Nat.	315	904	80.7		4.29	0.56	
1986	Hat.	258	859	68.7	.97	4.00	0.48	.94
	Nat.	538	889	79.4		4.24	0.54	
1987	Hat.	184	868	96.0	.96	4.05	0.69	.95
	Nat.	494	902	81.4		4.27	0.57	
OVERALL	Hat.	8	858	34.7	.96	4.05	0.34	.95
	Nat.	8	890	15.0		4.25	0.16	

Table D.5. Sex compositions of hatchery and natural Bright spawners. All ratios are computed as hatchery value divided by natural value; hence, ratios less than 1.0 indicate the hatchery value is the lesser. Hatchery spawners (Type = Hat.) were produced and coded wire tagged (see Appendix C) at Priest Rapids Hatchery. Brights spawning in the Hanford Reach are presumed, with some exceptions (see text), to have been produced naturally (Type = Nat.). Only records containing a length between 300 mm and 1500 mm and an age were used. Overall values are based on the unweighted of annual mean lengths for all 8 yr.

Return Year	Type	All Ages				Ages 3-6			
		n		%		n		%	
		Male	Female	Female	Ratio	Male	Female	Female	Ratio
1980	Hat.	68	106	60.9	.98	66	106	61.6	.97
	Nat.	584	971	62.4		556	970	63.6	
1981	Hat.	61	65	51.6	.76	39	65	62.5	.86
	Nat.	407	847	67.5		318	845	72.7	
1982	Hat.	57	45	44.1	.90	47	45	48.9	.88
	Nat.	1090	1055	49.2		835	1055	55.8	
1983	Hat.	60	36	37.5	.79	58	36	38.3	.76
	Nat.	1403	1271	47.5		1249	1269	50.4	
1984	Hat.	162	75	31.6	.75	121	75	38.3	.78
	Nat.	1738	1257	42.0		1268	1213	48.9	
1985	Hat.	644	154	19.3	.46	444	154	25.8	.50
	Nat.	442	315	41.6		299	315	51.3	
1986	Hat.	401	258	39.2	.90	209	258	55.2	1.04
	Nat.	698	538	43.5		477	538	53.0	
1987	Hat.	252	184	42.2	.94	252	184	42.2	.89
	Nat.	610	494	44.7		552	494	47.2	
OVERALL	Hat.	8		40.8	.82	8		46.6	.84
	Nat.	8		49.8		8		55.4	

Table D.6. Estimated mean fecundities of hatchery and natural Bright spawners. Ratios are computed as hatchery value divided by natural value; hence, ratios less than 1.0 indicate the hatchery mean is the lesser. Hatchery spawners (Type = Hat.) were produced and coded wire tagged (see Appendix C) at Priest Rapids Hatchery. Brights spawning in the Hanford Reach are presumed, with some exceptions (see text), to have been produced naturally (Type = Nat.). Only records containing a length between 300 mm and 1500 mm and an age were used; all females sampled in return years 1980-87 were included. Individual fecundities were estimated by $9.853L-3484.4$, where L is fork length in mm. The formula was derived from data collected from Brights spawned at Bonneville Hatchery in 1983, 1985, and 1986 (provided by D. Hankin, Humboldt State University, 1/89).

Type	All Ages		Ages 3-6	
	Mean Fecundity	Ratio	Mean Fecundity	Ratio
Hat.	4986	.96	4986	.95
Nat.	5219		5251	

Table D.7. Mean lengths at age and ratios of hatchery and natural Bright spawners. Ratios are computed as hatchery mean divided by natural mean; hence, ratios less than 1.0 indicate the hatchery mean is the lesser. Hatchery spawners (Type = Hat.) were produced and coded wire tagged (see Appendix C) at Priest Rapids Hatchery. Brights spawning in the Hanford Reach are presumed, with some exceptions (see text), to have been produced naturally (Type = Nat.). Only records containing a length between 300 mm and 1500 mm and an age were used.

Return Year	Age	Type	Male Length				Female Length			
			n	Mean (mm)	SD	Ratio	n	Mean (mm)	SD	Ratio
1980	2	Hat.	2	410	50.0	.91	0	-	-	-
		Nat.	28	449	77.5		0	-	-	
	3	Hat.	22	679	63.0	.98	3	757	74.1	1.00
		Nat.	216	690	86.9		51	756	67.7	
	4	Hat.	16	814	104.4	.91	16	869	67.9	1.01
Nat.		139	891	109.3	308		861	55.6		
5	Hat.	28	973	117.5	.92	87	934	87.0	.98	
	Nat.	201	1059	75.0		611	950	49.3		
1981	2	Hat.	22	461	63.0	.98	0	-	-	-
		Nat.	89	471	49.3		2	495	15.0	
	3	Hat.	13	645	86.6	.98	4	710	43.0	1.02
		Nat.	81	658	81.7		17	694	45.1	
	4	Hat.	20	815	127.7	.87	46	871	56.6	1.00
Nat.		194	934	82.7	645		873	52.8		
5	Hat.	6	990	75.3	.95	13	925	64.3	.99	
	Nat.	41	1040	56.3		176	931	60.2		

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Table D.7. (continued)

Return Year	Age	Type	Male Length				Female Length			
			n	Mean (mm)	SD	Ratio	n	Mean (mm)	SD	Ratio
1982	2	Hat.	10	445	47.4	.90	0	-	-	-
		Nat.	255	493	73.8		0	-	-	
	3	Hat.	35	752	73.9	1.09	23	743	36.5	.99
		Nat.	501	693	73.8		99	749	52.6	
	4	Hat.	10	828	107.9	.90	17	839	75.1	.98
		Nat.	255	918	96.2		608	858	64.0	
	5	Hat.	2	1070	30.0	.99	5	966	58.9	1.00
		Nat.	78	1076	67.0		348	962	53.5	
1983	2	Hat.	2	445	45.0	1.03	0	-	-	-
		Nat.	154	433	53.4		1	410	-	
	3	Hat.	34	631	54.4	.96	2	750	10.0	1.05
		Nat.	583	659	75.3		78	712	69.2	
	4	Hat.	24	916	106.9	1.00	34	875	46.9	1.01
		Nat.	602	916	103.9		1086	870	55.4	
	5	Hat.	0	-	-	-	0	-	-	-
		Nat.	63	1041	80.8		105	941	55.9	
1984	2	Hat.	41	424	26.8	1.00	0	-	-	-
		Nat.	470	423	46.9		44	421	46.1	
	3	Hat.	75	680	60.7	1.06	11	722	45.3	1.05
		Nat.	461	643	82.5		75	686	81.2	
	4	Hat.	43	867	91.8	.97	58	847	49.8	.97
		Nat.	650	896	94.6		874	875	60.3	
	5	Hat.	3	1040	37.4	1.01	6	962	88.0	.99
		Nat.	156	1033	75.0		264	967	54.5	

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Table D.7. (continued)

Return Year	Age	Type	Male Length				Female Length			
			n	Mean (mm)	SD	Ratio	n	Mean (mm)	SD	Ratio
1985	2	Hat.	200	481	36.6	1.06	0	-	-	-
		Nat.	143	453	55.6		0	-	-	
	3	Hat.	344	668	59.1	1.00	42	718	37.1	.97
		Nat.	150	667	73.8		18	743	50.9	
	4	Hat.	69	839	84.6	.93	82	852	45.2	.97
		Nat.	85	900	102.4		189	882	63.0	
	5	Hat.	30	1009	65.5	.95	30	920	62.9	.95
		Nat.	64	1067	68.0		108	969	47.9	
1986	2	Hat.	192	448	65.7	1.07	0	-	-	-
		Nat.	221	421	46.9		0	-	-	
	3	Hat.	114	684	55.3	1.04	28	750	51.1	1.07
		Nat.	249	658	70.0		23	700	59.9	
	4	Hat.	87	872	86.1	.95	204	862	49.8	.99
		Nat.	188	914	97.7		368	872	56.6	
	5	Hat.	7	964	99.4	.91	24	946	50.4	.98
		Nat.	37	1055	79.4		142	962	52.9	
1987	2	Hat.	0	-	-	-	0	-	-	-
		Nat.	58	447	62.5		0	-	-	
	3	Hat.	183	637	88.9	.99	39	726	51.4	.98
		Nat.	293	644	78.7		32	743	52.0	
	4	Hat.	56	890	87.8	.95	97	878	53.4	.99
		Nat.	180	932	93.9		298	883	60.9	
	5	Hat.	13	986	77.0	.94	48	963	42.7	.99
		Nat.	79	1054	89.9		164	968	52.2	

APPENDIX E

Data for Comparing Size and Age in Ocean and In-river
Fisheries to Size and Age in the Escapement

Table E.1. Mean ages for six coded wire tag (CWT) groups of Brights in fisheries and escapement. The most recent brood year used was 1980, so that recoveries of all broods were complete by 1987. AK = Alaska, BC = British Columbia, T = Troll fishery, N = Net fishery, Z1-5 = Zones 1 through 5 in-river gillnet fishery, Z6 = Zone 6 in-river gillnet fishery, ESC = Escapement to hatchery and natural spawning areas. (Raw data from S. Markey, WDF, Olympia, WA.) More information on CWT groups is in Appendix C.

CWT Code	AKT		AKN		BCT		BCN		Z1-5		Z6		ESC	
	n	Age	n	Age	n	Age	n	Age	n	Age	n	Age	n	Age
131101	109	3.96	2	4.00	128	3.95	129	4.69	50	3.98	68	4.06	245	3.89
131202	144	3.85	0	-	207	3.65	101	4.36	77	3.77	116	3.81	386	3.27
631662	24	5.12	4	4.50	65	3.98	106	3.75	10	3.50	35	3.97	71	4.00
631741	31	4.13	5	4.60	37	3.68	19	2.89	5	3.40	23	3.74	127	3.44
631948	77	4.14	19	3.58	27	3.70	3	2.67	10	3.70	21	4.05	148	3.39
632155	80	4.16	11	3.45	53	4.02	12	3.33	7	4.43	43	4.16	150	3.91

Table E.2. Mean lengths (mm) at age in the escapements of 14 coded wire tag (CWT) groups of Brights. Because of recent brood years (see additional CWT information in Appendix C), some groups lacked recoveries of older ages (indicated by dash) by 1987, the last recovery year compiled in this study. (Raw data from S. Markey, WDF, Olympia, WA.)

CWT Code	Age					
	3		4		5	
	n	Mean Length	n	Mean Length	n	Mean Length
131101	49	614	87	848	75	929
131202	80	671	137	849	41	972
631662	9	612	33	842	19	945
631741	25	688	66	854	7	996
631948	58	748	58	892	9	988
632155	36	638	66	850	35	955
632456	25	707	43	839	3	923
632611	118	674	110	863	20	981
632612	268	674	182	866	41	961
632848	44	695	54	877	-	-
632859	53	698	46	879	-	-
632860	46	696	53	891	-	-
632221	93	691	-	-	-	-
633222	69	689	-	-	-	-

Table E.3. Mean lengths (mm) at age and mean length ratios for 14 coded wire tag (CWT) groups of Brights taken in ocean and in-river fisheries. Ratios are fishery mean divided by escapement mean (from Table E.2); hence, ratios less than unity indicate smaller fish were taken in the fishery relative to the escapement. AK = Alaska, BC = British Columbia, T = Troll fishery, N = Net fishery, Z1-5 = Zones 1 through 5 in-river gillnet fishery, Z6 = Zone 6 in-river gillnet fishery. Because of recent brood years (see Appendix C), some groups lacked recoveries of older ages by 1987, the last recovery year compiled in this study. These are indicated by a dash (-) for sample size (n). (Raw data from S. Markey, WDF, Olympia, WA.)

Fishery	CWT Code	Age								
		3			4			5		
		n	Mean Length	Ratio	n	Mean Length	Ratio	n	Mean Length	Ratio
AKT	131101	3	694	1.13	100	775	.91	0	-	-
	131202	21	712	1.06	111	781	.92	0	-	-
	631662	0	-	-	0	-	-	21	885	.94
	631741	0	-	-	27	815	.95	4	900	.90
	631948	5	702	.94	48	821	.92	16	900	.91
	632155	3	674	1.06	51	776	.91	15	839	.88
	632456	4	698	.99	19	724	.86	0	-	-
	632611	4	652	.97	0	-	-	24	927	.94
	632612	14	665	.99	0	-	-	64	927	.96
	632848	0	-	-	53	839	.96	-	-	-
	632859	0	-	-	48	816	.93	-	-	-
	632860	0	-	-	38	831	.93	-	-	-
	633221	14	721	1.04	-	-	-	-	-	-
	633222	13	719	1.04	-	-	-	-	-	-

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Table E.3. (continued)

Fishery	CWT Code	Age								
		3			4			5		
		n	Mean Length	Ratio	n	Mean Length	Ratio	n	Mean Length	Ratio
AKN	131101	0	-	-	2	770	.91	0	-	-
	131202	0	-	-	0	-	-	0	-	-
	631662	2	555	.91	0	-	-	0	-	-
	631741	0	-	-	1	930	1.09	2	910	.91
	631948	3	623	.83	3	860	.96	0	-	-
	632155	2	615	.96	3	793	.93	0	-	-
	632456	0	-	-	1	750	.89	0	-	-
	632611	7	577	.86	0	-	-	0	-	-
	632612	15	603	.89	0	-	-	0	-	-
	632848	0	-	-	4	850	.97	-	-	-
	632859	0	-	-	0	-	-	-	-	-
	632860	0	-	-	2	775	.87	-	-	-
	633221	3	627	.91	-	-	-	-	-	-
	633222	0	-	-	-	-	-	-	-	-

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Table E.3. (continued)

Fishery	CWT Code	Age								
		3			4			5		
		n	Mean Length	Ratio	n	Mean Length	Ratio	n	Mean Length	Ratio
BCT	131101	28	665	1.08	0	-	-	21	885	.95
	131202	92	659	.98	0	-	-	18	863	.89
	631662	0	-	-	42	739	.88	9	868	.92
	631741	15	648	.94	19	783	.92	3	937	.94
	631948	11	665	.90	12	811	.91	3	957	.97
	632155	10	643	1.01	32	779	.92	10	881	.92
	632456	8	696	.98	9	823	.98	0	-	-
	632611	19	670	.99	0	-	-	8	950	.97
	632612	64	664	.99	0	-	-	47	940	.98
	632848	0	-	-	26	849	.97	-	-	-
	632859	0	-	-	33	836	.95	-	-	-
	632860	0	-	-	31	841	.94	-	-	-
	633221	29	704	1.02	-	-	-	-	-	-
	633222	32	698	1.01	-	-	-	-	-	-

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Table E.3. (continued)

Fishery	CWT Code	Age								
		3			4			5		
		n	Mean Length	Ratio	n	Mean Length	Ratio	n	Mean Length	Ratio
BCN	131101	8	596	.97	0	-	-	83	917	.99
	131202	13	592	.88	0	-	-	44	887	.91
	631662	0	-	-	66	751	.89	0	-	-
	631741	7	639	.93	4	810	.95	0	-	-
	631948	2	660	.88	0	-	-	0	-	-
	632155	3	583	.91	2	745	.88	3	890	.93
	632456	0	-	-	4	843	1.00	0	-	-
	632611	4	688	1.02	0	-	-	0	-	-
	632612	5	618	.92	0	-	-	2	995	1.04
	632848	0	-	-	2	895	1.02	-	-	-
	632859	0	-	-	0	-	-	-	-	-
	632860	0	-	-	1	950	1.07	-	-	-
	633221	3	613	.89	-	-	-	-	-	-
	633222	0	-	-	-	-	-	-	-	-

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Table E.3. (continued)

Fishery	CWT Code	Age								
		3			4			5		
		n	Mean Length	Ratio	n	Mean Length	Ratio	n	Mean Length	Ratio
Z1-5	131101	7	648	1.06	34	835	.98	8	890	.96
	131202	18	696	1.04	57	844	.99	2	935	.96
	631662	5	627	1.02	5	833	.99	0	-	-
	631741	3	619	.90	2	781	.91	0	-	-
	631948	4	748	1.00	5	808	.91	1	897	.91
	632155	0	-	-	4	737	.87	3	899	.94
	632456	9	655	.93	2	872	1.04	0	-	-
	632611	11	684	1.01	15	846	.98	8	966	.98
	632612	44	676	1.00	54	831	.96	28	956	.99
	632848	17	689	.99	24	869	.99	-	-	-
	632859	6	751	1.08	13	849	.97	-	-	-
	632860	7	689	.99	9	871	.98	-	-	-
	633221	14	707	1.02	-	-	-	-	-	-
	633222	23	730	1.06	-	-	-	-	-	-

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Table E.3. (continued)

Fishery	CWT Code	Age								
		3			4			5		
		n	Mean Length	Ratio	n	Mean Length	Ratio	n	Mean Length	Ratio
Z6	131101	12	662	1.08	42	869	1.02	12	970	1.04
	131202	29	714	1.06	80	836	.98	7	952	.98
	631662	10	639	1.04	16	820	.97	9	960	1.02
	631741	5	655	.95	16	841	.98	1	938	.94
	631948	2	751	1.00	16	851	.95	3	1007	1.02
	632155	7	660	1.03	24	827	.97	10	916	.96
	632456	8	712	1.01	20	840	1.00	6	886	.96
	632611	41	684	1.01	63	859	1.00	17	909	.93
	632612	75	689	1.02	219	843	.97	39	949	.99
	632848	32	705	1.01	52	864	.99	-	-	-
	632859	33	724	1.04	35	857	.97	-	-	-
	632860	17	684	.98	39	849	.95	-	-	-
	633221	20	706	1.02	-	-	-	-	-	-
	633222	38	709	1.03	-	-	-	-	-	-

APPENDIX F

Data for Comparing In-river Catch and Escapement:
Length, Age, and Sex Composition

Table F.1. Comparison of mean lengths in catches by in-river fisheries with escapement for Brights coded wire tagged as juveniles at Priest Rapids Hatchery, both sexes and all ages combined. Probabilities (P) are from the Mann-Whitney U test.

Return Year	Area/ Gear ^a	n	Mean Length (mm)	SD	P	Ratio ^b
1978	Z1-5	25	683	74	.02	1.06
	Z6	39	704	62	<.01	1.10
	Esc.	134	642	92		
1979	Z1-5	96	829	80	.32	1.03
	Z6	128	829	91	.40	1.03
	Esc.	257	805	184		
1980	Z1-5	19	817	158	.04	.93
	Z6	40	868	116	.27	.98
	Esc.	174	884	138		
1981	Z1-5	2	781	62	.60	1.01
	Z6	28	889	91	.01	1.15
	Esc.	126	776	186		
1982	Z1-5	5	766	100	.98	1.01
	Z6	11	785	120	.19	1.03
	Esc.	102	759	142		
1983	Z1-5	4	793	39	.79	1.01
	Z6	25	772	143	.60	.98
	Esc.	96	787	151		
1984	Z1-5	36	686	73	.02	.95
	Z6	74	740	134	.93	1.02
	Esc.	237	724	173		
1985	Z1-5	86	722	94	<.01	1.06
	Z6/U	105	739	126	<.01	1.09
	Z6/8	113	747	82	<.01	1.10
	Esc.	798	681	158		
1986	Z1-5	106	789	96	<.01	1.11
	Z6/U	126	823	106	<.01	1.16
	Z6/8	274	808	101	<.01	1.13
	Esc.	659	712	194		

- - continued - -

Table F.1. (continued)

Return Year	Area/ Gear ^a	n	Mean	Sample SD	P	Ratio ^b
			Length (mm)			
1987	Z1-5/U	70	813	108	.09	1.05
	Z1-5/8	51	893	101	<.01	1.15
	Z6	246	836	107	<.01	1.08
	Esc.	436	777	151		

^a Z1-5 = fishery, Zones 1 through 5; Z6 = fishery, Zone 6; /U = unrestricted mesh size; /8 = 8-in. minimum mesh size; Esc. = escapement.

^b Fishery mean length divided by escapement mean length; hence, ratios greater than unity indicate the fishery value is the greater.

Table F.2. Comparison of mean sizes and sex compositions in catches by in-river fisheries with escapement for Brights coded wire tagged as juveniles at Priest Rapids Hatchery, all ages. Probabilities (P) for lengths are from the Mann-Whitney *U* test; those for sex composition are from chi-square contingency tests using Yates' correction. Both tests compare the fishery sample to the escapement sample.

Return Year	Area/ Gear ^a	MALES					FEMALES					Sex Composition	
		n	Length				n	Length				Female	P
			Mean (mm)	SD	P	Ratio ^b		Mean (mm)	SD	P	Ratio ^b		
1978	Z1-5	14	664	82	.17	1.06	11	707	59	.63	.98	44.0	<.01
	Z6	19	678	60	<.01	1.08	20	728	64	.98	1.01	51.3	<.01
	Esc.	115	629	91			19	719	43			14.2	
1979	Z1-5	37	836	112	.02	1.17	59	825	53	<.01	.95	61.5	.52
	Z6	33	816	149	.04	1.14	95	833	61	<.01	.96	74.2	<.01
	Esc.	112	713	235			148	864	102			57.6	
1980	Z1-5	7	695	196	.06	.84	12	888	69	.05	.97	63.2	1.00
	Z6	9	823	184	1.00	1.00	31	880	88	.02	.96	77.5	.07
	Esc.	68	824	176			106	919	92			60.9	
1981	Z1-5	0	-	-	-	-	2	781	62	.07	.89	100.0	c
	Z6	12	930	114	<.01	1.39	16	859	56	.25	.98	57.2	.75
	Esc.	61	668	206			65	877	80			51.6	
1982	Z1-5	3	788	130	.36	1.09	2	732	49	.26	.91	40.0	c
	Z6	5	746	164	.40	1.03	6	816	67	.42	1.01	54.5	.73
	Esc.	57	723	163			45	804	93			44.1	

- - continued - -

Table F.2. (continued)

Return Year	Area/ Gear ^a	MALES					FEMALES					Sex	
		n	Length				n	Length				Composition	
			Mean (mm)	SD	P	Ratio ^b		Mean (mm)	SD	P	Ratio ^b	% Female	P
1983	Z1-5	0	-	-	-	-	4	793	40	.02	.91	100.0	c
	Z6	13	765	184	.50	1.04	12	779	85	<.01	.90	48.0	.47
	Esc.	60	739	170			36	868	55			37.5	
1984	Z1-5	24	666	65	.54	.99	12	727	74	<.01	.87	33.3	.99
	Z6	36	708	161	.36	1.05	38	771	96	<.01	.92	51.4	<.01
	Esc.	162	672	180			75	838	79			31.6	
1985	Z1-5	42	676	78	.03	1.05	44	767	88	<.01	.93	51.2	<.01
	Z6/U	60	685	126	.04	1.06	45	811	83	.23	.98	42.9	<.01
	Z6/8	72	728	80	<.01	1.13	41	781	75	<.01	.94	36.3	<.01
	Esc.	644	645	150			154	829	87			19.3	
1986	Z1-5	47	756	113	<.01	1.22	59	816	69	<.01	.95	55.7	<.01
	Z6/U	60	794	128	<.01	1.29	66	849	75	.43	.99	52.4	<.01
	Z6/8	140	786	125	<.01	1.27	134	831	61	<.01	.97	48.9	<.01
	Esc.	401	618	192			258	859	69			39.2	
1987	Z1-5/U	31	807	133	<.01	1.14	39	817	85	<.01	.94	55.7	.05
	Z1-5/8	27	872	121	<.01	1.23	24	916	67	.02	1.06	47.1	.61
	Z6	123	810	124	<.01	1.14	123	861	79	.22	.99	50.0	.06
	Esc.	252	711	151			184	868	96			42.2	

(footnotes on following page)

Table F.2. (continued)

^a Z1-5 = fishery, Zones 1 through 5; Z6 = fishery, Zone 6; /U = unrestricted mesh size; /8 = 8-in. minimum mesh size; Esc. = escapement.

^b Fishery mean length divided by escapement mean length.

^c Insufficient sample size for statistical test.

Table F.3. Comparison of mean sizes and sex compositions in catches by in-river fisheries with escapement for Brights coded wire tagged as juveniles at Priest Rapids Hatchery, ages 3-6. Female statistics for length are the same as in Table F.2. Probabilities (P) for lengths are from the Mann-Whitney *U* test; those for sex composition are from chi-square contingency tests using Yates' correction. Both tests compare the fishery sample to the escapement sample.

Return Year	Area/ Gear ^a	Males					Sex Composition		
		n	Length			Females			
			Mean (mm)	SD	P	Ratio ^b	n	%	P
1978	Z1-5	14	664	81	.25	1.04	11	44.0	<.01
	Z6	19	678	60	<.01	1.06	20	51.3	<.01
	Esc.	110	637	85			19	14.7	
1979	Z1-5	37	836	112	.99	1.03	59	61.5	.71
	Z6	32	829	133	.98	1.02	95	74.8	.06
	Esc.	82	815	201			148	64.3	
1980	Z1-5	6	726	195	.11	.87	12	66.7	.87
	Z6	9	823	184	.89	.98	31	77.5	.09
	Esc.	66	836	163			106	61.6	
1981	Z1-5	0	-	-	-	-	2	100.0	^c
	Z6	12	930	114	<.01	1.18	16	57.1	.77
	Esc.	39	785	161			65	62.5	
1982	Z1-5	3	788	130	.62	1.01	2	40.0	^c
	Z6	4	817	51	.23	1.04	6	60.0	^c
	Esc.	47	782	107			45	48.9	
1983	Z1-5	0	-	-	-	-	4	100.0	^c
	Z6	12	797	150	.31	1.06	12	50.0	.42
	Esc.	58	749	163			36	38.3	
1984	Z1-5	24	666	65	<.01	.88	12	33.3	.71
	Z6	31	753	123	.82	1.00	38	55.1	.02
	Esc.	121	756	124			75	38.1	
1985	Z1-5	39	688	68	.37	.96	44	53.0	<.01
	Z6/U	52	713	110	.50	.99	45	46.4	<.01
	Z6/8	71	730	77	.01	1.02	41	36.6	.02
	Esc.	444	719	120			154	25.8	

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Table F.3. (continued)

Return Year	Area/ Gear ^a	Males					Sex Composition		
		n	Length			Females			
			Mean (mm)	SD	P	Ratio ^b	n	%	P
1986	Z1-5	44	773	95	.83	1.00	58	56.9	.85
	Z6/U	58	803	120	.09	1.04	66	53.2	.76
	Z6/8	129	810	96	<.01	1.13	134	51.0	.30
	Esc.	209	773	124			258	55.2	
1987	Z1-5/U	31	807	133	<.01	1.14	39	55.7	.05
	Z1-5/8	27	872	121	<.01	1.23	24	47.1	.61
	Z6	123	810	124	<.01	1.14	123	50.0	.06
	Esc.	252	711	151			184	41.3	

^a Z1-5 = fishery, Zones 1 through 5; Z6 = fishery, Zone 6; /U = unrestricted mesh size; /8 = 8-in. minimum mesh size; Esc. = escapement.

^b Fishery mean length divided by escapement mean length.

^c Insufficient sample size for statistical test.

Table F.4. Comparison of mean sizes and sex compositions of Brights caught by in-river fisheries with and without minimum mesh size restrictions, all ages. Code groups are fish tagged as juveniles at Priest Rapids Hatchery (PRH) or at McNary Dam by the National Marine Fisheries Service (NMFS). See Appendix C for tag codes used. Probabilities (P) for lengths are from the Mann-Whitney *U* test; those for sex composition are from chi-square contingency tests using Yates' correction.

Return Year & Code Group	Area/ Gear ^a	MALES					FEMALES					Sex Composition %	
		n	Mean (mm)	SD	P	Ratio ^b	n	Mean (mm)	SD	P	Ratio ^b	Female	P
1985 PRH	Z6/8 Z6/U	72 60	728 685	80 125	<.01	1.06	41 45	781 811	74 82	.09	.96	36.3 42.9	.39
1985 NMFS	Z6/8 Z6/U	38 19	766 738	143 159	.65	1.04	39 25	866 866	89 95	.83	1.00	50.6 56.8	.64
1986 PRH	Z6/8 Z6/U	140 60	786 794	124 126	.79	.99	134 66	831 849	61 74	.08	.98	48.9 52.4	.59
1986 NMFS	Z6/8 Z6/U	45 13	885 869	100 125	.56	1.02	78 22	866 876	65 55	.55	.99	63.4 62.9	1.00
1987 PRH	Z15/8 Z15/U	27 31	872 807	119 131	.07	1.08	24 39	916 817	66 84	<.01	1.12	47.1 55.7	.45

^a Z15 = fishery, Zones 1 through 5; Z6 = fishery, Zone 6; /U = unrestricted mesh size; /8 = 8-in. minimum mesh size.

^b mean length for 8-in. minimum mesh divided by mean length for unrestricted mesh; hence, ratios greater than one indicate the 8-in. mean is the larger.

Table F.5. Comparison of mean sizes and sex compositions of Brights caught by in-river fisheries with and without minimum mesh size restrictions, ages 3-6. Code groups are fish tagged as juveniles at Priest Rapids Hatchery (PRH) or at McNary Dam by the National Marine Fisheries Service (NMFS). See Appendix C for tag codes used. Probabilities (P) for lengths are from the Mann-Whitney *U* test; those for sex composition are from chi-square contingency tests using Yates' correction.

Return Year & Code Group	Area/ Gear ^a	MALES					FEMALES					Sex Composition	
		n	Length				n	Length				% Female	P
			Mean (mm)	SD	P	Ratio ^b		Mean (mm)	SD	P	Ratio ^b		
1985 PRH	Z6/8 Z6/U	71 52	730 713	77 109	.01	1.02	41 45	781 811	74 82	.09	.96	36.6 46.4	.20
1985 NMFS	Z6/8 Z6/U	38 19	766 738	143 159	.65	1.04	39 25	866 866	89 95	.83	1.00	50.6 56.8	.64
1986 PRH	Z6/8 Z6/U	129 58	810 803	96 118	.78	1.01	134 66	831 849	61 74	.08	.98	51.0 53.2	.76
1986 NMFS	Z6/8 Z6/U	45 13	885 869	100 125	.56	1.02	78 22	866 876	65 55	.55	.99	63.4 62.9	1.00
1987 PRH	Z15/8 Z15/U	27 31	872 807	119 131	.07	1.08	24 39	916 817	66 84	<.01	1.12	47.1 55.7	.45

^a Z15 = fishery, Zones 1 through 5; Z6 = fishery, Zone 6; /U = unrestricted mesh size; /8 = 8-in. minimum mesh size.

^b mean length for 8-in. minimum mesh size divided by mean length for unrestricted mesh value; hence, ratios greater than one indicate the 8-in. mean is the larger.

APPENDIX G

Run Reconstructions and Selection Differentials for
Length in the In-river Fisheries.

(Reference for cited source is listed with those from the text, p. 191.)

Table G.1. Calculations to estimate the number of all ages (including jacks) in the escapement and fisheries, 1984-87, based on numbers of adults estimated for those years. Estimated adults from ODFW and WDF (1988); samples are from coded wire tag recoveries (sources described in text).

Year	Est. No.	Sample		Adjusted No.
	Adults (A)	All Ages (B)	Jacks (C)	All Ages [A/(1-(C/B))]
<u>Zones 1-5</u>				
1984	23,700	36	0	23,700
1985	34,500	86	3	35,747
1986	58,900	106	3	60,616
1987	104,300	121	0	104,300
<u>Zone 6</u>				
1984	29,000	75	5	31,071
1985	54,300	218	9	56,638
1986	90,100	401	13	93,119
1987	120,000	264	0	120,000
<u>Escapement</u>				
1984	61,200	238	41	73,937
1985	90,700	800	201	121,135
1986	113,000	663	194	159,742
1987	154,000	436	0	154,000

Table G.2. Reconstructed runs and selection differentials (S) for length in the in-river fisheries, 1984-87, all ages. Adjusted numbers of fish are from Appendix Table G.1; sample mean lengths are taken or calculated from coded wire tagged fish summarized in Appendix Table F.1. Lengths are mm. Rounding causes some apparent mathematical discrepancies.

Year	Escapement		Zone 6				
	(A) Adjusted Number	(B) Mean Length	Catch		Entering the Fishery		Fishery S (B-F)
			(C) Adjusted Number	(D) Mean Length	(E)	(F)	
					Est. Number (A+C)	Est. Mean Length (AB+CD)/E	
1984	73,937	722	31,071	743	105,008	728	- 6
1985	121,135	682	56,638	743	177,774	701	-19
1986	159,742	712	93,119	813	252,861	749	-37
1987	154,000	777	120,000	836	274,000	803	-26

Year	Escapement		Zones 1-5					
	(A) Adjusted Number	(B) Mean Length	Catch		Entering the Fishery		Fishery S (F-J)	Overall S (B-J)
			(G) Adjusted Number	(H) Mean Length	(I)	(J)		
					Est. Number (E+G)	Est. Mean Length (EF+GH)/I		
1984			23,700	686	128,700	720	8	2
1985			35,747	722	213,520	705	- 3	-23
1986			60,616	789	313,476	757	- 8	-45
1987			104,300	846	378,300	815	-12	-38

Table G.3. Reconstructed runs and selection differentials (S) for length in the in-river fisheries, 1984-87, ages 3-6. Estimated numbers of fish are from ODFW and WDF (1988); sample mean lengths are taken or calculated from coded wire tagged fish summarized in Appendix Tables F.2 and F.3. Lengths are mm. Rounding causes some apparent mathematical discrepancies.

Year	Escapement		Zone 6				
	(A) Estimated Number	(B) Mean Length	Catch		Entering the Fishery		Fishery S (B-F)
			(C) Estimated Number	(D) Mean Length	(E)	(F)	
					Est. Number (A+C)	Est. Mean Length (AB+CD)/E	
1984	61,200	784	29,000	763	90,200	777	7
1985	90,700	747	54,300	753	145,000	749	- 2
1986	113,000	821	90,100	823	203,100	822	- 1
1987	154,000	777	120,000	836	274,000	803	-26

Year	Escapement		Zones 1-5					
	(A) Estimated Number	(B) Mean Length	Catch		Entering the Fishery		Fishery S (F-J)	Overall S (B-J)
			(G) Estimated Number	(H) Mean Length	(I)	(J)		
					Est. Number (E+G)	Est. Mean Length (EF+GH)/I		
1984			23,700	686	113,900	686	19	26
1985			34,500	730	179,500	746	4	1
1986			58,900	797	262,000	816	6	5
1987			104,300	846	378,300	815	-12	-38

APPENDIX H

Data for Bright Run Timing

Table H.1. Mean dates of Bright jack and adult run timing at The Dalles Dam. Data compiled and summarized by B. P. Lumley, Columbia River Inter-Tribal Fish Commission, Portland, OR.

Year	Jacks			Adults		
	Mean Day of Year	Mean Date	SD	Mean Day of Year	Mean Date	SD
1962	246.3	9/4	15.9	251.3	9/9	12.4
1963	249.3	9/7	13.6	252.5	9/10	14.3
1964	245.6	9/4	12.9	251.3	9/9	11.3
1965	248.6	9/7	11.7	251.3	9/9	11.2
1966	250.3	9/8	13.8	255.0	9/13	13.3
1967	254.1	9/12	12.8	254.6	9/13	14.0
1968	251.9	9/10	15.3	250.2	9/8	13.5
1969	251.1	9/9	11.9	253.3	9/11	11.4
1970	248.4	9/6	13.1	251.6	9/10	12.6
1971	256.4	9/14	12.9	252.3	9/10	11.0
1972	254.2	9/12	13.0	253.2	9/11	13.1
1973	253.1	9/11	14.5	252.2	9/10	11.8
1974	261.1	9/19	15.3	255.8	9/14	12.0
1975	251.2	9/9	16.2	253.0	9/11	12.3
1976	259.5	9/18	15.0	252.5	9/11	12.9
1977	257.8	9/16	13.5	255.3	9/13	14.7
1978	262.4	9/20	15.5	255.5	9/13	14.7
1979	253.5	9/12	14.1	253.9	9/12	17.2
1980	257.5	9/16	15.1	256.3	9/14	15.8
1981	258.2	9/16	13.9	251.2	9/9	14.2
1982	256.2	9/14	13.9	256.8	9/15	14.8
1983	264.4	9/22	13.7	258.1	9/16	14.9
1984	263.0	9/21	14.2	252.0	9/10	13.6
1985	257.6	9/16	12.6	254.6	9/13	14.6
1986	263.2	9/21	12.0	256.6	9/15	13.0
1987	261.8	9/20	14.4	255.6	9/14	12.7